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The Role of Territory in Bird Life[1]

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The theory of territory in bird life is briefly this: that pairs are spaced through the pugnacity of males towards others of their own species and sex; that song and display of plumage and other signals are a warning to other males and an invitation to a female; that males fight primarily for territory and not over mates; that the owner of a territory is nearly invincible in his territory; and finally that birds which fail to obtain territory form a reserve supply from which replacements come in case of death of owners of territories.

Definitions

Neither of the founders of the theory—Altum or Howard—gave a strict definition of what they meant by "territory." Recently, however, several definitions have been proposed. For example, Mayr (1935) gave the following:

"Territory is an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous."

"Sexual territory" is defined by Tinbergen (1939c) as "an area that is defended by a fighting bird against individuals of the same species and sex shortly before and during the formation of a sexual bond."

Finally, Crawford (1939) explains territorialism as follows: "A limited geographical area is settled upon and defended by an animal, usually a male, and is used by him for mating and rearing of a family."

Noble's definition (1939) that a "territory is any defended area" is in my opinion the most satisfactory because it is so simple and inclusive.

The reason for the spacing of pairs is still disputed. According to one of the earliest theories its "purpose" is to ensure an adequate food supply for

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2 I am indebted to David E. Davis, Lawrence E. Hicks, S. Charles Kendeigh, Ernst Mayr, Joost ter Pelkwyk and Charles F. Walker for helpful suggestions.

the young. On the other hand, one writer suggests that the function of territory is the prevention of the undue increase of the species; another thinks it may be a precaution against disease; still others say it is merely a matter of the male's "song-center," while a fourth group suggests it may offer protection against despotism and interference in the orderly sequence of the nesting cycle.

Obviously the territory theory is a revolutionary view point. Even quite recently most bird students believed that males fought over mates, and that the "purpose" of singing was to charm the mate. Moreover, there was no conception of the fixity of territory, since it was taken for granted that pairs were free to wander where they wished at any time during the breeding season in search of suitable nesting sites. These statements may well be true of some species, notably those nesting in holes, but it is now known that they do not apply to the majority of passerine birds in Europe and America. In this connection it is illuminating to note the consistently pre-territorial viewpoint of Dawson's "Birds of California" (1921) and Forbush's "Birds of Massachusetts" (1926-29).

Historical Sketch

That males of many species of birds refuse to allow other pairs of the same species to settle in close proximity has been known for a long time. The earliest recorded instance seems to have appeared in 1622 in relation to the Nightingale *(Luscinia megarhyncha)*, as pointed out by Alexander (1936):

In Ray's *Ornithology of Francis Willughby*, 1678, (p. 222), we find:—

'It is proper to this Bird at his first coming (saith Olina) to occupy or seize upon one place as its Freehold, into which it will not admit any other Nightingale but its mate.'[3]

This is one of the passages added by Ray to the English edition and does not occur in the Latin edition of 1676. The statement by Olina, of which it is a translation, occurs on page 1 of his *Uccelliera*, first published in 1622, and reads:—

'Nel suo arrivo hà per proprio il pigliarsi un luogo, come sua franchigia, nel quale non ammette altri Russignuoli, che la propria femmina, e in quello d'ordinario canta.'

It will be seen that Ray omitted this last statement that 'it ordinarily sings in its freehold.'[4]

The next record is cited by Ticehurst ('34), who states that the territory idea was a well recognized fact by our ancestors at least three hundred years ago, in the case of, at any rate one species, the Mute Swan. Section 21 of 'The orders Lawes and Ancient Customes of Swanns', printed by order of John Witherings in 1632, but based on others at least fifty years older still, reads:

'And yet neither the Master of the Game, nor any Gamster may take away any swanne which is in broode with any other mans, or which is coupled, and *hath a walke*, without the other's consent, for breaking the brood.' The italics are mine.

Gilbert White of Selborne wrote in 1772 (but not publishing the letter until 1789):

3 The Century Dictionary gives the definition of "freehold" as, "Originally, in England, an estate in land in possession held by a freeman; a. . feudal estate. ."

4 Material is 8 point type is quoted.

During the amorous season such a jealousy prevails amongst the male birds that they can hardly bear to be together in the same hedge or field. . . . It is to this spirit of jealousy that I chiefly attribute the equal dispersion of birds in the spring over the face of the country.

Two years later Oliver Goldsmith even used the word territory.

The fact is, all these small birds mark out a territory to themselves, which they will permit none of their own species to remain in; they guard their dominions with the most watchful resentment; and we seldom find two male tenents in the same hedge together.

In 1820 Johann Friedrich Naumann stated:

The male usually arrives first; he seeks a breeding place and suffers no other pair to nest within a certain distance.

There are two early descriptions of territory in hummingbirds. In 1825 Bullock wrote of the Lucifer Hummingbird *(Calothorax lucifer)*, "When attending their young, they attack any bird indiscriminately that approaches the nest. . . . They attack the eyes of the larger birds, and their sharp, needle-like bill is a truly formidable weapon in this kind of warfare. Nothing can exceed their fierceness when one of their own species invades their territory during the breeding season." In 1877 Henshaw states in regard to Allen's Hummingbird *(Selasphorus alleni)*, "Each male seems to claim a particular range, which he occupies for feeding and breeding purposes, and every other bird seen by him encroaching on his preserve is at once so determinedly set upan and harrassed that he is only too glad to beat a hasty retreat."

The first ornithologist to grasp the essentials of the territory theory was Bernard Altum. In his remarkable book *Der Vogel und sein Leben*, first published in 1868, the seventh edition appearing in 1903, the territory theory is given in detail. The following selections are taken from the translation by Mayr ('35).

It is impossible among a great many species of birds, for numerous pairs to nest close together, but individual pairs must settle at precisely fixed distances from each other. The reason for this necessity is the amount and kind of food they have to gather for themselves and their young, together with the methods by which they secure it. All the species of birds which have specialized diets and which, in searching for food—mostly animal matter—for themselves and their young, limit their wanderings to small areas, cannot and ought not to settle close to other pairs because of the danger of starvation. They need a territory *(Brutrevier)* of a definite size, which varies according to the productivity of any given locality.

Pairs of different species frequently nest close together. Several pairs of the same species, however, which live on the same kind of food and employ the same manner of securing it, cannot nest together; they must necessarily be separated by established boundaries.

What separates them? It is, of course, natural that the most suitable localities will be most sought by the species preferring them. Large numbers will gather in such places, over-crowding them, while other available territories would be empty if pairs were not kept apart by force. This force is used by a male as soon as another gets too close during the breeding season. The interloper is immediately attacked in the most violent manner, and driven to a distance that is determined by the size of the required territory.

But many of my readers will ask what is the connection of song, the main subject of this chapter, with the question of territory? A bird must be able to perceive another bird in order to know of his presence. The majority of the above-mentioned birds, however, for example, all of our Sylviae, Phylloscopi, Reed-warblers, Larks, Kinglets, Titmice, etc., live in dense scrubs or thick luxurious vegetation. Since birds cannot detect each other by their olfactory sense, as mammals do, they must make themselves conspicuous in some other manner, i.e., by their mating call, their song. If birds were more or less mute, a too close approach would rarely be noticed by them, and even if it were noticed and the intruder driven the proper distance away, he could soon come back silently and unnoticed. As it is, however, since all birds sing zealously, this is not possible, for every time a bird approaches too closely, it is at once attacked again. They sing day after day, in the morning and evening continuously, and by this song the boundaries of the territory are fixed. In fact, the real fight, the mutual attack of the males, is frequently begun while they sing, and the song continues during the battle. . . . The song, or mating call, is thus the necessary means for the required separation of the territories.

Some species of birds, have no definite territories. On a single tower a hundred pairs of Jackdaws may nest, one Martin nest may be built on the side of another, and under the roof of a large house we can find dozens of nests of House Sparrows and Swifts. The arctic sea birds, Auks, Murres, Puffins, Gulls, and Terns, and also the Cormorants, Herons, Rooks, Starlings, and others nest more or less colonially, some of these in groups of many thousands.

We have learned in the important previous chapter that the song and mating call of the male birds has among other things not only the purpose of indicating from the distance to the females, (which react only to the voice of the males of their own species), their often rather hidden station, but it also serves in many species as a mutual signal, to fix the distance of the nests and thus the required size of the territories, since males which happen to get too close to each other fight until one of the combatants has retreated to the required distance.

In short even the expression 'fighting of the males over females' is false: The males fight to fix the size of the territory, little as they realize the vital necessity of this, and also to select the healthiest individuals for reproduction, but for nothing else.

Thus Altum stated all the essentials of the territory theory, including the modern view of song as a threat to other males and invitation to a female. In addition he thoroughly believed in the food value of territory. Altum was far ahead of his time and although his theories were generally accepted in Germany, they were not known in other countries.

Another early exponent of the territory theory, C. B. Moffat in Ireland, was also overlooked. His interesting paper, published in 1903 and republished in 1934, is well summarized in his letter in the January 1934 number of *British Birds:*

My contention, when writing on the 'Spring Rivalry of Birds,' was that the battles of the male birds, each claiming a territory, resulted in such a parcelling out of the land as must limit the number of breeding pairs to a fairly constant figure, and prevent indefinite increase in the case of any species—at the same time condemning the less powerful individuals to unproductiveness rather than to death.

In the paper of 1903 Moffat emphasizes the fact that the fighting is for territory and not for mates. In discussing the theory of sexual selection, he says:

The song and bright plumage of a cock-bird are, on this theory, the charms by which he establishes his place in the heart of her to whom he pays court. But how do they help him to win a plot of ground? . . . The chief and primary use of song, then,

as I conceive it, is to advertise the presence in a certain area of an unvanquished cock-bird, who claims that area as his, and will allow no other cock-bird to enter it without a battle.

He then suggests that "the bright plumage may have been originally evolved as 'war paint' . . . as a sort of 'warning coloration' to rival males, rather than attractive colouration to dazzle the females."

The point that Moffat stresses most is his idea regarding the function of territory. He makes no mention of food value, but considers that

in the course of time, the country—or the parts of it suitable for nidification—would come to be completely parcelled out between the birds, each parcel of land belonging to a particular pair; I mean, as against any other pair of the same *kind*. And once this happy state was arrived at, the number of nesting pairs each year would be exactly the same, the number of nests and the average number of young birds reared would be exactly the same; and whether there was a large mortality in winter, or a small mortality in winter, the total number of birds in the country would remain exactly the same.

He believes that there are a very large number of unmated birds of both sexes present, perhaps on "land left where the beaten birds can find plenty of food and shelter, though not adapted for nesting," and that these birds fill vacancies in the ranks of the breeders. He does not believe in any great mortality in birds. "It seems to me, despite all perils, a large proportion, amounting in some species to a majority of those that leave their nest, live."

Moffat's idea that the function of territory is the prevention of undue increase of the species seems a little far-fetched. He is too optimistic when he believes that most young that leave the nest survive; banding has shown us that most of them die within the first year. Neither has his notion of a large population of unmated birds waiting on the outskirts for vacancies in the ranks of those in possession of territories, been corroborated by field studies.

In 1906 William Brewster gave a brief statement of the territory theory:

I have observed—as, indeed, who has not!—that few birds—excepting those which, like Swallows, Terns, Herons, and Gulls, are accustomed to nest in colonies—tolerate very near neighbors of their own species during the season of reproduction. At its beginning each pair takes possession of a definite tract of woodland, orchard, swamp or meadow, which the male is ever on the alert to defend against trespassers of his kind and sex, although he often seems quite willing to share his domain with birds of other and perhaps closely related species. The extent of the area thus monopolized varies exceedingly with birds of different species. . . . Whatever the extent of the domain, the birds who occupy it as a summer home evidently regard it as exclusively their own. The readiness and celerity with which trespassing birds are accustomed to retire when attacked or even merely threatened by the established tenants, has seemed to me to indicate that the claims of temporary ownership are respected by all right-minded birds. . . . In my opinion the desire for exclusive possession so conspicuously shown by the male, and often by him alone, is usually the direct result of *sexual jealousy*. . . . If his concern were chiefly in respect to the food supply, it would be equally manifested at every season and towards all birds who subsist on the same food that he and his mate require—which is certainly not the case.

In 1912 Francis Herrick published a pioneer paper on the Herring Gull (*Larus argentatus*). This account, as he notes later (1935), "written in 1903 but not published until six years later, gave the first intimation so far as I

know of the importance of breeding territory in relation to any bird." He reported that:

> The herring-gull community is made up of family units, and the breeding-ground of family domains, each of which I shall call a *preserve*, any given pair of birds choosing their territory and guarding it with relentless vigilance. Upon each preserve are situated: (1) the nest, (2) the perch, (3) the favorite feeding-spot, and (4) the favorite cover of the chicks. Each domain is determined primarily by the nest, and secondarily by the other elements in the family establishment. There may be more than one perch; feeding-spots may shift, but the fighting disposition, upon which the guarding largely depends, is early in evidence and does not lapse until after the young take to the water.

Two other Americans mentioned features of territorial behavior. Althea Sherman (1910) suggested that the "determining factor" in the spacing of pairs of the Northern Flicker *(Colaptes auratus luteus)* might be "the area necessary for their food collection." A. A. Allen (1914) wrote of the male Red-winged Blackbirds *(Agelaius phoeniceus)*, "From their first arrival, they assume all rights to the domain on which they have established themselves."

In 1919 Henry Mousley discussed the headquarters of the males in relation to the nests. In a later paper (1921) he wrote:

> It (the 'singing tree') is surely the home of the male bird, where he awaits the coming of his bride, the place from which he loves to sing, and so in time it becomes the loadstone which eventually guides her to him. It also acts as a lookout post, from which he can perceive any encroachment on his domain and at once resent it by immediately attacking the intruder, which is plain to be seen almost any day during the breeding season.

Thus Mousely stated some of the elements of the territory theory, but did not go into the matter deeply.

The ornithologist with whom the concept of territory will always be linked is the Englishman, H. Eliot Howard. In "The British Warblers," published between 1907 and 1914, the territorial idea appears throughout and is summarized in the final section. Unfortunately, few ornithologists outside of Great Britain were acquainted with this work. In 1920 his volume "Territory in Bird Life" appeared; this book has had an immense influence on bird students throughout the world. His later "Introduction to the Study of Bird Behaviour" (1929) gave further stimulus to serious investigators, but its distribution was curtailed by its cost.

Although Howard was not acquainted with the work of Altum nor the paper by Moffat, his theory closely follows that enunciated by the distinguished German ornithologist. Howard's theory of the function of territory postulates that the pairs are spaced in order to insure an adequate supply of food for the young. This is effected in the following manner: the male bird "isolates himself, makes himself conspicuous, becomes intolerant of other males and confines his movements to a definite area" (1929).

Howard claimed that the whole cycle of behavior in the breeding season centres around territory; it ensures that the male should obtain a mate; it

serves as a focus for the pair before the nest is built; it "certainly serves to promote an ample supply of food for the young near the nest"—an important provision in unfavorable weather. The "establishment of territories serves so to regulate the distribution of pairs that the maximum number can be accommodated in the minimum area." The fighting for a territory ensures that only the strongest males succeed in reproduction.

In addition to the application of the theory to the typical territory of Reed Buntings, Warblers, etc., Howard extended his theory to include colonial nesters. In the case of many sea birds, food is unlimited, but nesting sites are few, hence a minimum of nesting space is all that can be allowed each pair in the interests of the species.

In a letter to Ernst Mayr, Oct. 6, 1935, Howard explains the underlying basis of his theory:

> My starting point was, and still is, the congenital foundation which is expressed by a male occupying a region and at the same time becoming intolerant of other males within that region. When a Guillemot occupies a bit of ledge long before an egg is laid and drives away intruders, or a Ruff occupies a station on the meeting ground and drives away intruders, there is no difference, as far as I can see, in the congenital foundation. From this congenital foundation have grown regions of different sizes with different proximate ends; but neither size nor end change the congenital foundation.

Howard's great service was emphasis. His work aroused an immense amount of interest and thus became the starting point of a new period in the study of the behavior of birds.

In general, the theory of territory, as presented by Howard, has been received enthusiastically and has been rejected only by a few.

Some ornithologists—Alexander (1921), Jourdain (1927) and Nicholson (1928)—thought that Howard erred through over-enthusiasm in trying to make colonial species fit into the pattern. Nicholson believes that Howard "has done at least as much to further the study of birds as any other living person" (1934), yet he points out exceptions to the "rule" of territory.

He writes in his stimulating book "How Birds Live" (1929) that "when this territorial instinct is developed, which insists that the male shall at all costs secure and hold a territory adequate to feed his offspring, the danger of overcrowding is removed." Nevertheless, "a more varied or a less precarious food supply, a sparse population, or a serviceable pair of wings may all bring emancipation from a system which is undoubtedly a strain and an oppression to the birds that are forced to live under it. The swallow is an example of a small, purely insectivorous species which, by its exceptional powers of flight, is released from the obligation of keeping exclusive territory and permitted to live with impunity in little settlements." He also mentions Martins, Swifts and Starlings as birds not needing territory.

I cannot agree that territory is a "strain and oppression to the birds that

are forced to live under it." Thas is not the impression I have gained from finding a Song Sparrow all winter long in his territory, which he is unwilling to leave or defend.

The "great food-shortage delusion" appears "ludicrous" to Lord Tavistock, who wrote in the Ibis (1931), "Ascertain the territory of a particular Willow-Warbler; then search carefully for insect-food of a kind palatable to Willow-Warblers; on a mere fraction of the bird's domain even dull human vision will discover enough small creatures to sustain a dozen Willow-Warblers." (I have often wished that I could find such a happy hunting ground; in my endeavors in Massachusetts, Ohio, Illinois, Michigan and Austria to find insects for baby birds, I have come to have the greatest respect for the abilities of parent birds.) He points out the Peregines on the sea-coast with "teeming hordes of sea-birds" in their vicinity, Grouse and the limitless expanse of heather, and the case of Swans and Geese, scoffing at the idea that any of these need to fear food shortage.

To explain the facts of territory, he brings forward a novel idea. "So widespread an instinct as the pugnacity of breeding-birds, is, however, likely to have some practical value to the species, and I suggest that it operates as a *check on disease*." He mentions epidemics among Wood-Pigeons, Rooks, Starlings, Game-birds, House Sparrows, Penguins and "cliff-breeding birds in Iceland," while "Among the majority of unsocial species it (disease) is almost unknown." (Nevertheless many of these social birds are among our most successful species.)

In the meantime, what actual studies were being made on the subject of territory? At first very few.

In 1910 Brock published a paper on "The Willow-Wrens of a Lothian Wood" which, on the whole, corroborated Howard's observations, but in which he noted that the female sometimes nested outside her mate's territory.

Five years later an interesting paper by Dewar (1915) on the Oystercatcher appeared in which he stated that

> each pair has an habitual range in a nesting area and in a local feeding-ground. The boundaries, where the range of one pair meets those of adjacent pairs, are elastic; depending, in part, on the presence or absence, at the moment, of the adjoining pairs. Each station, composed of the breeding area and the local feeding-ground, has a headquarters generally, but not always, situated in a small eminence between the two areas. At the headquarters the birds keep watch and issue challenges. All other birds of the species are driven from the breeding area and the local feeding-ground.—The general or distant (neutral) feeding-ground is apparently common property. All the birds of a district appear to be free of the arable land near the breeding territories, and mingle without signs of hostility.

In 1922 A. H. Hamer proposed an independent version of the territory theory, emphasizing the function of warning colors in the proclamation of territory in place of fighting.

> The purposes fulfilled by territorialism are one or both of the following, (1) the conservation of a food supply, (2) the jealous reservation of the female partner or

partners. . . . Observation shows that the morale bestowed upon the possessor by settled possession of territory appears among birds to be irresistible.

Pioneer work on life history and territorial relationships was done by J. P. Burkitt in Ireland on the Redbreast *(Erithacus rubecula)*, the birds being distinguished by *colored* bands. This is a strongly territorial species; "A male normally retains the whole or part of his breeding territory throughout the year and from year to year." Females hold territory by themselves during the winter, while the young take up their territories as early as mid-June, July and August.

Methods of making and using colored bands were investigated further by W. K. Butts (1927, 1930, 1931) in connection with his studies of the summer and winter territories of the Chickadee *(Penthestes atricapillus)* and White-breasted Nuthatch *(Sitta carolinensis)*. By now the use of colored bands has become a basic technique in any intensive study of territory.

Valuable work was done on the Prairie Horned Lark *(Otocoris alpestris praticola)* by Pickwell (1931), who graphically describes the aerial battles of neighboring males. Other important papers about this time describe territorial behavior in the Marsh Hawk (Errington, 1930), European Blackbird (Heyder, 1931), California Shrike (Miller, 1931b) and Bullock Oriole (Miller, 1931a), and several Greenland birds (Nicholson, 1930). The first of Mrs. Laskey's excellent studies on color-banded Mockingbirds *(Mimus p. polyglottos)* appeared in 1933.

Lack (1932) found unexpected inconsistencies in expected territorial behavior in the European Nightjar *(Caprimulgus europeus)*. Interestingly enough, Friedmann (1929) after studying Cowbirds in North and South America, based his theory of the origin of parasitism in these birds on a weakening of the territorial urge.

The first comprehensive review of the subject of territory covering the pioneer work of Altum and the contributions of 41 authors was published by Wilhelm Meise in 1930. The next was my own review, "The Theory of Territorialism and its Development" (1933), in which I traced the history of the subject, described the territorial behavior in the Song Sparrow and discussed various theoretical aspects. This was followed by a similar article in French (Nice, 1934) and by a detailed description of territory in the Song Sparrow (Nice, 1933 and 1934).

In December 1933 David and Lambert Lack published an important paper, entitled "Territory Reviewed" in which they protested against the uncritical acceptance of the territory theory. The authors point out that the same species may at times "appear territorial" and at other times nest in colonies, instancing the Great Black-backed Gull, Great Crested Grebe, and "many Birds of Prey"[5] which "are normally colonial under favorable condi-

[5] "That birds of prey can and do live in colonies abroad is such a well-known fact that we need only mention Lesser Kestrels, Red-footed Falcons, Black Kites, Eleonoran Falcons, Griffon Vultures, etc., as instances. Some of these birds are quite as communal in their breeding habits as the Rook." Jourdain (1927).

tions." As to the food value of territories, they state that "most territorial species, which are extremely pugnacious at the beginning of the breeding season, do not attempt to maintain strict territories during the feeding of the young—that is, at the very time that the territories, as food territories, would be most valuable. . . . Finally, it is not proved that pugnacity does limit the number of pairs in a given area."

Their alternative theory is: "In fact, territory seems to be nothing more than an affair of the male bird, and its real significance seems to be that it provides him with a more or less prominent, isolated headquarters where he can sing or otherwise display."

The Lacks' statement that "so far sufficient evidence has not been adduced to show that territory is a general law of bird life, and that in especial there is no proof that territory is of food value, or is an important factor in the prevention of overcrowding" has stimulated critical observation. These authors did a distinct service in pointing out problems to be investigated. Territory —in a wider sense—has now been shown to be a fairly general law of bird life; in some cases it is of food value, and in others it prevents over-crowding.

Although Selous never read Howard's "Territory in Bird Life," he devotes two chapters in "Evolution of Habit in Birds" (1933) to the question "Are Birds Really Landed Proprietors?" The following quotation (p. 153) suggests that he made the problem more difficult than necessary. "Before either a man or a bird can privately appropriate even the narrowest space of land, meaning to resist any other attempt at occupancy thereof because of its own prior right of possession, there must be a conception in the mind of each of what such right personal possession with consequent effects really is." He claims also that birds do not appropriate sources of food to themselves, but many of us are familiar with despotic behavior of individuals at feeding shelves, e.g., Moore (1939) records the intolerance of the White-eared Hummingbird *(Hylocharis leucotis borealis)* towards Hummingbirds of all other species that attempted to use its preferred food plants.

In "A Natural Experiment on the Territorial Instinct" Julian Huxley (1934) described the behavior of Coots *(Fulica a. atra)* and Mute Swans *(Cygnus olor)* on a pond during winter.

> In their paper the Lacks state that 'there is no real evidence that the pugnacity of the male sets a definite limit to the number of pairs in a given area.' In the case of these Swans it would certainly appear that it was doing so. The pugnacity of the male (and to a lesser extent that of the female) is clearly seeing to it that one pair of Swans shall grow where two pairs grew before.

Ritter and Benson (1934) described the "shadow boxing" of a male Brown Towhee *(Pipilo fuscus petulans)*, showing the astonishing amount of energy expended by this bird in defense of his territory and concluded:

> It is now certain that several species of resident birds in California keep, and defend to some extent, their territories throughout the year and for several years.

A novel, but unconvincing, explanation of the purpose of territory was given by A. A. Allen (1934):

> Bird behavior, . . . selection of territory, song, fighting, and display of plumage are explainable on the basis of the necessity for synchronizing the mating cycles of male and female.

Interesting observations were made by Col. and Mrs. Ryves on the Corn-Bunting *(Emberiza c. calandra)* (1934, a and b); the males "take possession of a suitable territory, hold it against all comers and advertise themselves by constant singing"; the singing perch commands "a view of the nest site," or where the male has several mates, "he will so place himself as to command at least one nest and the route or routes to the feeding grounds of his other hen or hens." All the nests are placed within the male's territory, but feeding takes place 600 yards or more away.

Venables (1934), describing the behavior of Dartford Warblers *(Sylvia undulata)* during the latter part of the nesting season, found some pairs apparently strictly territorial, but where the birds were more abundant, territories were "shared, apparently without any friction, between two or three pairs."

Concerning the St. Kilda Wren *(Troglodytes troglodytes hirtensis)* Harrison and Buchan (1934) reported the average size of territories to be 3,000 to 5,000 square yards, but food was collected in only a very small portion of each territory, about 2.6 per cent. Moreover, each parent tended "to feed in exclusive food patches not used by the other."

Venables and Lack (1934) found that some pairs of the Great Crested Grebe *Podiceps c. cristatus* were intolerant and other colonial—all in the same pond. They wrote:

> Territorial behaviour is clearly correlated with the position of the nest. Even the colonial pairs sometimes attacked other individuals which came too close to their nests. This habit seems merely to have become greatly exaggerated in the territorial pairs. The effect of this behaviour was to render uninhabitable for other pairs reed-beds which could otherwise have been utilized for nests. . . . The territory is not correlated with the food supply. . . . Territorial behaviour must definitely be reckoned as one factor affecting the density of the breeding population.

In 1935 Ernst Mayr translated the portions of Altum's book concerning territory, and proposed in his discussion of the subject of territory the following definition: "Territory is an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous." This definition disregards the "purpose" of territory and omits "winter territories" as well as those cases in which females hold territories (such birds "apparently belong always to species of highly unsocial character and fighting disposition"). On the other hand, it includes nest-territories of certain social birds and mating stations of Ruffs, etc., and what might be called typical territory. Finally, after discussing the questions of food-value and sex-jealousy, Mayr makes the following suggestion regarding the evolution of territory: "Territory was originally developed only in connection with the mating, but it has acquired in certain passerine species a secondary significance as the food providing area."

The Micheners (1935) found that color-banded Mockingbirds

> have two general types of territories, summer territories and winter territories. . . . The winter territory centers about the food supply and is defended by both the male and the female, in case the pair remains together, or by the lone male or female occupant. . . . The defense of the winter territories seems much more vigorous than that of the summer territories. . . . The female rarely takes part in the defense of the summer territory.

A most interesting situation is reported by N. Tinbergen (1935) in the case of the Northern Phalarope. In this species it was the female that proclaimed and defended territory and performed a ceremonial flight accompanied by repeated "love-calls" over her territory.

> As soon as the bird discovered another Phalarope in the neighborhood, either a male or a female, she at once performed the ceremonial flight, in the direction of the newcomer. If it was a female, she would soon attack; if it happened to be a male, she would court him.

The first detailed study on territory in a tropical bird was made by David Lack (1935) on the Crimson-crowned Bishop-bird *(Hordacea hordacea)*, a species in which the gorgeously colored male is polygamous. It was found that

> territory is as well developed in the male *hordacea* as in any known bird, and far more rigid than in many so-called territorial species. . . . Clearly the territory bears no relation to the food-supply of the young, since the female obtains almost all the food for the young (and also for itself) from well outside the territory. . . . The value of the territory is probably to achieve isolation for the cocks, and so to assist the hens to find mates. . . . I formed the impression that the bright colors, the song, and the display were used solely in advertising and defending the territory, in the manner postulated by Howard.

In "Further Notes on Territory in the Great Crested Grebe" Venables and Lack (1936) conclude:

> Aggressive behaviour resulting in a 'territory' is exhibited by only a few individuals, the majority tolerating other individuals close to a nest. . . . The territory is not of primary significance in pairing up, as many pairs are formed before they acquire a territory; but a male does at times acquire and defend a territory before obtaining a mate. The territory does not usually include the feeding ground of the pair, and is in all cases deserted when the young hatch. . . . The territory is associated with the neighbourhood of the actual or future nesting platforms, but does not seem of benefit to the species in this connection. The territory seems to be an individual affair, of no fundamental significance to the species.

The Nuttal White-crowned Sparrow *(Zonotrichia leucophrys nuttalli)* pairs stay permanently on their territory. Barbara Blanchard (1936) discusses the continuity of territorial and sex relations in this species in California, describing a family where the male had two mates. Each female "created for herself a sub-division of the main territory which she defended *against the other female* by loud singing and fighting, and in which she finally chose her nest site. . . . Had they not been banded," writes the author, "I should have thought I was watching a boundary dispute between two males."

In one of the most significant contributions to the theory of territorialism N. Tinbergen (1936) writes: "The problem of the function of 'territory' originated as the problem of the function of fighting of male birds in spring."

Darwin "concluded that the fighting of male birds in spring was 'over the females,' and that a female would choose a strong and victorious male in preference to a weak male to mate with." Tinbergen explains how a moose fights in the vicinity of the herd of females wherever they may be, while with a fish, *Rhodeus amarus*, which lays its eggs in the gills of a mussel, the male "settles in the neighborhood of a mussel, and fights furiously against other males of the same species, thereby actually 'defending' this mussel. . . .

The fighting before and during the formation of sexual bonds, therefore, serves to secure objects or situations which are indispensable for reproduction. . . .

In most birds, territory is included as one element in this situation, as a consequence of their laying in a certain place, eggs which have to be incubated in that same place. In most birds, the sex partner is another element of the situation. In the Moose, the sex partner is the only element. In *Rhodeus*, the mussel is one element, the female another one.

He mentions how, in the Snow Buntings, the fighting of females against females, as well as the fighting of the males, "serves as a means of establishing monogamy, and monogamy is biologically most important in connection with the rearing of the young."

In opposition to many ornithologists who disclaimed territory in the case of colonial birds, Tinbergen asserts:

A colonial bird may be just as territorial as a solitary bird. . . . In the Grey Heron, for instance, the territory is a place where a nest can be built, Verwey; a territory of a Kestrel is a place where a nest is present, L. Tinbergen; in Howard's Buntings, as well as in the Snow Bunting, the territory must contain something more, and the question of the food for the young certainly is of importance, though it is yet impossible to see its exact value.

It is true that much of territorial fighting takes place before the arrival of the female.

But as a female is attracted only by a male in full sexual condition, and a male in full sexual condition has a territory, a territory is, to the male, 'a potential female'; it is absolutely the same (functionally), if a female is present in the territory at once, or if it will be present after some time.

In 1936 Meise published another excellent review of the subject of territory, discussing the question from many angles and incorporating the results of recent studies; his bibliography included 66 titles.

Winter quarrels over territory were reported by Morley (1936) for Moorhens *(Gallinula ch. chloropus)* in Sussex, and for Mockingbirds by Laskey (1936). In a notable study on the biology of the Herring Gull *(Larus a. argentatus)* Goethe (1937) found that many of the birds arrived paired and at once took up their territories.

An important study on a highly territorial bird, the Wren-tit *(Chamaea f. fasciata)*, was carried out by means of colored bands by Mary Erickson in California (1938). Territory is held throughout the year, and singing is heard at all seasons.

The territorial habit limits the number of individuals in a given area. In Hamilton Gulch, in the course of a year, an average of twelve or thirteen locations was all that became available for about thirty-three young wren-tits. Whether or not possession of a territory is essential to the success of the individual life, it is unquestionably essential to reproduction. The ultimate competition is for space.

William Vogt (1938b) found that "The willet is a *highly territorial* bird and guards the boundary of its demesne, through much of the breeding season, as vigorously as does any passerine." The birds, however, are paired before claiming territory, and the male defends his mate before he defends territory. Territory is proclaimed by a spectacular ceremonial flight in which the male, "rapidly and loudly calling *pill-will-willet*" rises high in the air, circling about and flickering the tips of the wings "like tongues of black and white flame." The Willet is highly socialized and disregards "all territorial boundaries when repulse of an enemy is involved."

An important contribution to the theoretical aspect of territorial behavior, especially as it concerns colonial birds, was made by Konrad Lorenz in 1938. I will quote from his paper later.

Another significant study of territory in tropical birds should be mentioned—that of the Moreaus (1938) on two species of Biship-Birds in East Africa. The Zanzibar Red Bishop *(Euplectes nigroventris)* and Crimson-crowned Bishop *(E. h. hordacea)*, weavers of the subfamily Ploceinae, are polygamous, the males holding territory and building foundation nests for their mates.

In neither species does the size or position of the territory bear any relation to the availability of food for adults or young, or to topographical features. In *E. hordacea* (studied by Lack) "size of territory is possibly specific. *E. nigroventris* on the other hand is almost indefinitely compressible. . . . Its territories vary in size from 9 to at least 1,000 sq. yd. . . . At the height of the nesting season there is always suitable ground unoccupied. But territories containing no food and suffering the maximum of disturbance from other species can be found crowded together more closely than territories in areas possessing neither of these disadvantages. . . .

Irrspective of the size of his territory, a male *E. nigroventris* has up to five breeding females active in it at once and may raise eight families in it during the season. In a territory of *E. hordacea* not more than three breeding females have been found at once. . . . In one species the specific territory size can, on present evidence be regarded as a limiting factor in population density, while in another, closely allied and with generally similar habits, this possibility is excluded. In the 'compressible' species the suggestion of any food motive in the territorial habit can be ruled out with exceptional conclusiveness. Finally, the smallest territories of the 'compressible' species are not obviously less successful than any others of either species.

In his theoretical discussion of the "Role of Dominance in the Social Life of Birds," Noble (1939) claims that

sexual territory is a direct consequence of the nest-building habit in vertebrates. . . . The future parents must associate together, react in common if bonds are to be formed which will hold them as a pair during the entire breeding season. . . . Sexual territory . . . arises from the sexual interest of the animal in an area suitable for nesting and it functions primarily to test sexual readiness of the opposite sex and to make possible the formation of sexual bonds. Sexual territory is not to be confused with a nesting territory which has a different motivational basis, nor with an isolated retreat which is defended by many vertebrates against intruders at any season.

In a study of dominance in the Canary, Shoemaker (1939) reports that "Birds subordinate in neutral territory become dominant in their nesting territory."

In his valuable paper on color-banded Robins *(Erithacus rubecula)* Lack (1939b) analyzes the factors of aggressive and territorial behavior. Territory is held by the male throughout the year, while some "females hold autumn territories with fighting and song." A bird trying to claim new territory "often commences with extremely quiet song from the secondary growth"; later there may be loud singing from both owner and new-comer, alternated with chasing. "Although the possession of a territory would appear to be vital to a male Robin for success in reproduction, in all six cases the encounter was concluded without any fighting in the true sense being observed. Such formal and 'psychological fighting' is one of the most remarkable facts of bird behaviour. The singing in these contests is the finest of the year."

Tinbergen's (1939c) important study of the Snow Bunting *(Pletrophenax nivalis subnivalis)* in Greenland records all events from the first arrival of the males in spring to the independence of the young. The warning function of the ceremonial flight was shown by the cowering of a trespassing male. Mated males stopped singing and did not resume it until nesting was under way; mated males were more aggressive than unmated (as Howard found with the Reed Bunting and Lack with the Robin), while female Snow Buntings fought other females. A scholarly discussion on the functions of sexual fighting, of territory, "advertising song," etc., is appended.

Hickey (1940) describes how male American Redstarts *(Setophaga ruticilla)*

> advertised their presence by their typical well-known song and by formalized territorial displays that apparently served to define boundaries and reduce fighting. These displays consisted of short, horizontal, semi-circular flights made with stiffened wings and outspread tails.

Although the English Robin "sings and fights only in its own territory, it frequently trespasses for food." After "pair-formation the pair usually enlarge their territory, and since an unmated male is much less aggressive than a mated one, this expansion is usually at the expense of unmated neighbours" (Lack, 1940a).

In regard to Yellow-headed Blackbirds *(Xanthocephalus xanthocephalus)*, Fautin (1940) writes:

> Although very intolerant of each other within the confines of their personal territories, the males were very cooperative in times of danger. . . . The purpose of territory in this species seems to me: a. To insure adequate nesting sites. b. To aid the females in obtaining mates. c. To afford protection from various interferences during nesting season.

The European Wren *(Troglodytes tr. troglodytes)* defends territory all the year by song and posturing except during the molt in August and the severest winter weather (Kluijver et al., 1940).

Experiments on "The Inner Territory of the Black-headed Gull" were carried out by Kirkman (1940). Nests were never placed nearer than 18 inches to each other from center to center; when moved nearer by the experimenter, "The same bird that in one experiment played the part of the territory owner, full of assurance and pugnacity, became in the next, as intruder, all hesitation and timidity." In the case of *Larus ridibundus* "territory follows the nest-egg situation."

The "mildness of temper" of most Central American birds is discussed by Skutch (1940): "Where birds have the entire year in which to adjust conflicting territorial claims, to settle amorous disputes, they may gradually come to an understanding without resort to violence." A great many birds in this region live in pairs the year around.

According to Rand (1940) Macgregor's Bird of Paradise *(Macgregoria pulchra)* is usually seen in pairs in the Snow Mountains in New Guinea; the

> Species is monogamous. But the male does not establish a territory. Six birds were seen to indulge in sexual flight in the area in which a nest was found in construction six days later, and during three days of observation during the construction of this nest seven to eight birds in all were giving their sexual flight in the immediate vicinity of the nest, sometimes as close as twenty yards to it.

In his fine study of the Gentoo Penguin *(Pygoscelis papua)* Roberts (1940) writes:

> As the snow disappears, the nest sites provide circumscribed areas of great emotional valency, and display becomes confined almost entirely to these areas. . . . The fights are between neighbours with adjoining territories, or with trespassers which come too near the nest. Any bird, of either sex, which comes too near will excite a territory-defending reaction.

The best description that we have of a communal territory is given by Davis (1940a) for the Smooth-billed Ani *(Crotophaga ani)*. "Each flock of *C. ani* possesses a definite territory which it defends against strangers. The boundaries are well known to the members of the colony and are not passed. The individuals cannot be driven from their territory, even when pursued by a man. . . . The chasing, rushing, and fighting to defend the territory are very fierce. The impulse to defend is so strong that the birds fight a stranger even while a man is at the nest." A communal nest is built. Sex and food are not factors involved in the communal territory. "The characteristics of the territory behavior of *C. ani* show clearly that the defence of the piece of land is the important feature. . . . The defence of territory in *Crotophaga* . . . is merely an extension of the defense of the nest site.

With *Guira guira*, "Evidence indicates that the flock maintains a territory although pairs, which nest simultaneously even when they belong to the same flock, may maintain a territory. In three cases pairs from the same flock built nests simultaneously, while in four cases the flock built a communal nest." (Davis, 1940b).

Types of Territory

One of the chief controversies concerning territorialism arose from the varied use of the term "territory." Altum included only those cases in which all the activities of the pair were confined to the territory, whereas Howard regarded it as a general law of bird life. This is one of the main points on which Howard was criticized by Jourdain, Nicholson, the Lacks, Mayr, myself and others. Tinbergen, however, states that "A colonial bird may be just as territorial as a solitary bird," and Lorenz (1938) says that territorial behavior is "extremely prominent in the colony-nesting Herons." I have now come to accept this view.

In 1935 Mayr classified "Space occupied by individual birds" into four categories:

> I. Mating station and feeding ground for young. . . . True territory.
>
> II. Mating station, but not feeding ground. (a). Connected with nest. . . . (b). Not connected with nest. . . .
>
> III. Not mating station, but feeding ground (Males and females of certain species between breeding seasons).
>
> IV. Restricted to nest, no significance in regard to mating or feeding of young. (a). Colonial species. . . . (b). Solitary species. . . .

I adopt this classification in its main features, raising, however, one subdivision to the rank of division, adding one class, and reversing the order of the last two, as follows:

A. Mating, nesting, and feeding ground for young.

B. Mating and nesting, but not feeding ground.

C. Mating station only.

D. Restricted to narrow surroundings of nest.

1. Colonial species.
2. Solitary species.

E. Winter territories.

F. Roosting territories.

Some birds are hard to fit into any of these categories; for instance the Kingbird *(Tyrannus tyrannus)* (Davis, 1941b) and Black-capped Chickadee (Odum, 1941) mate before choosing territory; the former feeds outside the territory, the latter inside; the former makes itself conspicuous, the latter does not.

Type A

Mating, Nesting, and Feeding Ground for Young

This is the classic example of territory as described by Altum and Howard. It might be subdivided according to the length of occupation, whether it is held all year or only for the breeding season.

This type is known in many species:—Reed and Snow Buntings, Song, Field, White-crowned, Chipping and other Sparrows, many Old World Warblers, many Wood Warblers, Prairie Horned Lark, Wrens, Meadowlark, Orioles, Mockingbird, Robin Redbreast, Wood Thrush, Towhees, Shrikes, Wren-tit, Dipper, Woodpeckers, Kingfishers, Phalarope, Ani, etc.

As an example let me describe that of the bird with which I am most familiar—the Song Sparrow.

From March, 1928 to February, 1936, I banded with colored and aluminum bands 343 adult Song Sparrows on their territories on Interpont, some 40 acres of flood plain between our house and the Olentangy River in Columbus, Ohio, during 1929 laying the foundation for these population studies by an intensive study of two pairs. About half the males proved to be permanent residents, while the others (and the majority of the females) migrated south in October, returning from late February to early April according to the weather.

The resident male Song Sparrow stays on or near his territory throughout the year, although he does not defend it during the molt or in winter. In the autumn he drives off any young male that tries to settle on it, but does not object to the presence of other members of his species. The summer resident stays on his territory throughout his stay here. Both sets of males sing to some extent in the autumn after the molt—some very little, others much. Males defend their territories most vigorously at the beginning of the season, i.e., from the first warm spell in late January or in February on, till nesting begins in April. But until mid-July they are ever ready to drive off any new male that tries to intrude.

Territories are about three-quarters of an acre in size. In the winter a male will extend his range over a district from six to ten times as large as the breeding territory. In cold and snowy weather birds might come considerable distances for brief visits to my feeding station, even a quarter of a mile from their territories.

Some of the juvenile resident males may take up their territories in September and October and there remain for the rest of their lives. Others try to do the same, but are driven out by the adult owner on the completion of his molt. Still others apparently do not attempt to settle down until February. As for the summer residents, some at least choose their territories during their first autumn and in the spring return to a definite area, which they claim as their own, if possible.

Female Song Sparrows never hold territories for themselves, in contrast to the Redbreast, California Shrike, Mockingbird and some Woodpeckers. Nor do males drive off their mates at the end of the nesting season as Burkitt found with the Redbreast. The resident female winters in the vicinity of her nesting territory but does not necessarily associate with her former mate at this time. Each Song Sparrow is rather independent during autumn and winter, but not aggressively solitary, as the species mentioned above.

The female learns the boundaries of her mate's territory and usually accepts them, although in 1929 one built her nest in her neighbor's territory, causing her mate a great deal of difficulty until he was finally able to annex that portion for himself (Nice, 1939a). Females defend the home territory from neighboring females and males, and—like their mates—also from many other species of birds.

Since territory constitutes the basis of most of the Melospizan behavior in this region, it is natural that the procuring and defending of territory should have a definite technique consisting of song, display and combat. The bird in possession of a territory signifies the fact, as is well known, by his loud song, which is repeated five to seven times a minute from a conspicuous perch. But when a new male appears with intent to settle next door, or perhaps to appropriate a portion of the first bird's territory, or even to take it entirely, then the owner's behavior changes at once and the procedure of territory establishment begins. One of the birds sings constantly, eight to ten times a minute, usually puffed out and sometimes vibrating a wing, while the other, silent and menacing, follows him closely. After a while the silent bird starts to chase the singer, but the latter always returns to the piece of land he covets. Finally there is a fight on the ground, after which the birds separate and each sings triumphantly on his own territory, unless, indeed, the new-comer is thoroughly beaten and chased away.

This is the complete pattern, but there are countless variations according to the seriousness of the participants, while the roles may be changed as the contest progresses. It may happen that the less serious the encounter, the greater is the posturing, as Howard maintains (1929): in these ceremonial affairs the chase and fight are omitted.

Song Sparrows, especially the males, return to or remain on their territories year after year. Some males kept exactly the same territories year after year. Others made some change of territory; often the new and old partly coincide but at other times they do not. In some cases this may be due to the exigencies of the situation a summer resident finds on his arrival; occasionally an old bird adopts a slightly different territory rather than driving out the birds already established. But a resident or an early summer resident may shift his territory somewhat with no pressure from other birds, nor from change in environment, the longest of such moves being 100 meters.

The female that has nested before tries to return to her former home, but often this is impossible because another bird has preëmpted her place. In such

cases she often settles next door, but sometimes joins a male at a distance of 200 to even 700 meters, even though there may be unmated males near her old territory.

In 54 instances involving 41 birds I know the territories of females two years in succession; 20 of these were the same both years, 16 were neighboring territories, in nine cases the birds moved about 100 meters, in seven from 150 to 250 meters, in two 400 meters, and one 700 meters.

As to birds banded in the nest, 22 males took up territories from 100 to 1,400 meters from their birth places, the average being 280 meters; while 12 females settled from 45 to 1,300 meters from their birth places, the average being 270 meters.

Whereas song is now regarded as being intimately connected with territory, few other subjects of avian behavior appear in a similarly modified light, since the acceptance of Howard's theory. Dawson (1923) mentions the two chief pre-territorial theories concerning the meaning of song: "If bird-song expresses, as we hold, joy in life, rather than merely a passing desire to capture a mate, then is the Mockingbird the most joyful of birds." Fourteen years later, after a careful study of many color-banded individuals of the same species, the Micheners concluded that "little if any of their singing is merely for the pleasure of creating the song or is an expression of peace and contentment with the surrounding world, but rather that all songs, or at least most songs, are uttered for vital, practical purposes." Altum's and Howard's claims, that song is a warning to other males and an invitation to a female, are now accepted together with those of Nicholson (1929) that "song is the expedient used by inconspicuous birds to compensate for the drawbacks of being inconspicuous"; of Howard, who believes that song was "evolved primarily for the purpose of recognition" (1920, p. 142); and of Nicholson (1929:54) that "song, arising as a spontaneous expression of the emotions, was, in the case of those species which embraced individual territory, captured by what may be called the territorial set of instincts and developed intensively as their expression."

These theories are based on the fact that the typical territory song is short and simple, and that many species have at the same time a quite different "sub-song," "rambling and interminable" (Nicholson), which everyone agrees is the earlier form. I have observed with the greatest interest, in the young resident Song Sparrow, the actual process of the evolution of the sub-song into the territory song under the stimulus of territory situations.

The song of the adult Song Sparrow is short, lasting from two to three seconds with seven to nine second intervals between the end of one song and the beginning of the next. The song of the juvenal male in fall, winter, and very early spring is warbling, prolonged and lacking in any definite form. In February a young bird on his territory may be singing in this fashion, but upon the appearance of an adult male bent on territory establishment, the

song changes character and becomes approximately adult in form. After the departure of the rival, the young bird resumes his warbling. Once territory is definitely taken up by mid-February or in March, all of the singing is adult in character. Juvenile summer residents never warble after their arrival on their breeding grounds.

With the Song Sparrows on Interpont, territory definitely limits the number of pairs in a given area, as Tinbergen found with the Snow Bunting (1939c). Whenever a new male arrives, all the birds already settled in the vicinity try to drive him out, even though there may still be plenty of room. The new bird responds with appropriate behavior and soon wins his place. But there is a limit beyond which the birds will not allow themselves to be crowded; each must have approximately three-quarters of an acre for his territory and extra males have to seek other quarters. In 1932, when Interpont was filled to capacity, several of the young resident males were driven off of their territories upon the return of the former owners from the south.

Each pair supports itself and its young brood on its own territory. But food is evidently not the whole reason for territory with Song Sparrows: spacing of the pairs is essential to ensure non-interference in the orderly sequence of the nesting cycle. For the male Song Sparrow has the habit of "courting" in his peculiar rough way, neighboring females in the temporary absence of their mates. Territory seems to be a temperamental necessity as well as an economic one.

Moffat believes that there is a large reserve supply of unmated birds of both sexes, and as proof quotes some astonishing figures where mates were replaced in rapid succession. Recently a number of observers have found unmated males of many species *holding territory* (see Mayr, 1939). Zimmerman (1932) shot a small series of Red-backed Shrikes *(Lanius collurio)*, always one of a pair, three times the male, four times the female; in every case the survivor promptly found a new mate, yet the neighboring pairs were undisturbed. He suggests that there may be birds which do not mate until meeting with an especially strong stimulus such as would come from a bird that had just lost its mate.

On Interpont there was a slight preponderance of males in the Song Sparrow population, but the unmated males, almost without exception were settled on territories. There was a high mortality of breeding birds of both sexes during the nesting season, especially of females. Only three times did new males appear and join widows; in each case nesting was under way. Widowers sometimes obtained new mates promptly, but at other times had to wait for weeks and in many cases they sang in vain for the rest of the season. During six years the ratio of males to 100 females averaged 105 in April and 118 in June.

Thus it will be seen that the Song Sparrow fulfills Howard's scheme of a typical territorial passerine where all the food for the family is gathered on the territory and where territory does at times limit the number of pairs in a certain area.

Type B

Mating and Nesting, but Not Feeding Ground

In these cases territory is strictly kept as a matter of display ground, mating ground and nesting area, but much or all of the food for the adults and young is obtained off of the territory. Despite this distinction, I believe that Type B is closely related to typical territory.

Examples of this type are: Great Crested Grebe, Swans, Willet, Oystercatcher, Marsh Hawk, and among passerines, Red-winged and Yellow-headed Blackbirds, the two Bishop-birds studied by Lack and the Moreaus, and the Corn Bunting. The Eastern Goldfinch *(Spinus t. tristis)* sometimes comes under this category according to Drum (1939), but other observers can find no evidence of territory (Walkinshaw, 1938, 1939, Nice, 1939b).

Although the Scarlet Finch *(Carpodacus erythrinus)* feeds its young on regurgitated seeds, the birds are territorial (Haas, 1939) in some regions, males driving other males from their territories that extend 40-60 by 50-79 meters. When the author approached a nest, the parents scolded and several other males would appear; these the nest owner drove off, singing as he did so. Feeding was on neutral ground outside the territories; it lay 100-500 meters distant, in one case even 1000 meters.

Type C

Mating Station Only

In many species where the female takes sole charge of the nest and young, the males gather in *leks* for display and are visited here by the females. Each male has a small territory which he defends from other males.

Examples are: the Ruff, Prairie Chicken, Sharp-tailed, Sage and Black Grouse, Capercaillie, some Birds of Paradise, some Hummingbirds, Manakins.

The following quotation is taken from Frank Chapman's very interesting study "The Courtship of Gould's Manakin *(Manacus vitellinus vitellinus)* on Barro Colorado Island, Canal Zone" (1935). Each male makes himself a "court" by removing loose material from a small space on the forest floor. "Five to seven courts placed, usually about thirty to forty feet from each other, constitute a group or *lek*. This association of several males is more likely to attract the attention of the female than the efforts of a single bird.

"The vocal powers of the males are limited and, to announce the location of their courts to the females, they produce with their wing-feathers loud snapping and whirring sounds which can be heard at surprising distances. With rare, and generally explicable, exceptions territorial rights are rigidly observed. . . . Hence, once the female is in court, there is no competition for her favors. . . .

"The success of the *Manacus* system of courtship is based on a rigid observance of territorial rights. . . . Wider territory was claimed not only by the most sexually active bird, but, as might be expected, by the dominant bird. . . . "This recognition of boundaries makes for law and order. No time or energy is lost in futile disputes or needless conflicts and the birds may devote themselves to winning the attention of the female, now the chief object of their lives. . . .

"Under the normal conditions of courtship . . . the males are at peace with each other, not because they are of a peaceful disposition and do not know how to fight, but because they are so well organized and observe the laws of court-life so rigidly that the occasion for conflict does not arise."

Type D

Restricted to Narrow Surroundings of Nest, Both Colonial and Solitary Species

A very great number of species belong to this category, e. g. of colonial forms many sea-birds, Gulls, Terns, Cormorants, Murres, Penguins, Herons, some doves, Jackdaws, Starlings, some Swallows, etc.; of less colonial species, House Sparrows (Daanje, 1941) some Doves, some Swallows, many birds of prey, etc.

This type as exemplified by the Jackdaw and the Night Heron has been aptly described by Konrad Lorenz (1938).

There are two ways in which evolution can change the indubitably primitive territorial instincts so as to make colony-nesting possible. Either one common territory must be shared by all the birds of the colony, [as in the Jackdaws] or else the territories of individual pairs must shrink to such an extent that the nests can be built so closely together as to produce the outward appearance and advantages of a rookery. This latter possibility has been realized in the colony-breeding Herons and in a number of other birds. The nesting territory of a pair of Night-Herons has an area of but a few cubic feet, yet it retains all the characteristic features of the typical territory of other birds. Of course its extreme smallness makes it necessary for the birds to seek their food on some neutral ground, but many other birds do the same, as, for instance, according to Howard, the Yellow Bunting does. But the chief characteristic of territory is the fact that any individual will fight with very much more vigour if the combat is decided in his own territory. To my mind it has not been sufficiently emphasized that this increase of fighting power is not equal all over the ground defended by one individual bird, but that it always increases in proportion to how near a certain centre of the territory the fight takes place. This causes territories to 'behave' like pieces of elastic substance, the counter-pressure of which is proportional to the deformation caused by some outward influence.

After describing the boundary quarrels of the Stickle-back, Lorenz continues:

This esesntial phenomenon of territory is very much the same in a great number of territorial animals. It is extremely prominent in the colony-nesting Herons because of the small size of their territories and the correspondingly rapid increase of fighting power which takes place when the bird moves a few yards from the outer boundary of his territory to its centre. This increase more than compensates for any difference in vigour that may exist between two birds within the normal range of variation peculiar to the species. Naturally this protects the nests of even the weakest birds so effectively against the invasions of other Night-Herons that such wonderful instinctive reactions as those which guard the nests of Jackdaws are quite unnecessary and therefore absent.

Type E

Winter Territories

In this category I include only those territories which are located elsewhere from the bird's summer territory. Many birds under type A hold territory in winter as well as summer if permanently resident; this would seem to be an intensification of the territorial habit that extends the isolation to the non-breeding season. See Morley's account of Moor-Hens (1936), Burkitt's (1925) and Lack's (1939b) of Redbreasts, Miller's of Shrikes (1931b), Laskey's (1936) and Micheners' (1935) of Mockingbirds, Ritter's and Benson's of Brown Towhees (1934), Erickson's of Wren-tits (1938), Kluijver's of European Wrens (1940), Davis' of Anis (1940a) and Skutch's of Central American birds (1940).

Winter territory, i.e., an area used as a feeding ground and defended against other birds of the species resembles typical territory, but differs from all the four previous types by the absence of the sexual situation. The bird may show Howard's "isolation," "fixation," and "intolerance," but no "advertisement."

Price (1933) reports that two partially albino Western Robins *(Turdus migratorius propinquus)* resorted each day for a month during the winter to a small area from which they drove other Robins, while each evening they flew to a common roost four miles distant.

On the beach at La Jolla, California, in winter each Black-bellied Plover *(Squatarola squatarola)* (Michael, 1935), "claimed and held for his very own a strip of perhaps a hundred yards. No other Black-bellied Plover was permitted to encroach, but shore-birds of other species were allowed to forage freely." If a neighbor "comes into his domain" he "ruffles his neck feathers, crouches into a belligerent attitude and trots towards his enemy as though to butt him from the premises. His bluff always seems to work, as no blows are ever struck."

Type F

Roosting Territory

The probability that each individual Starling *(Sturnus vulgaris)* returns at night to its special "nook or cranny" on buildings at Washington, D. C., was discussed by Kalmbach (1932). Later definite evidence was adduced by Rowan (1938) when he found that the space occupied by 40 Starlings, collected from the center of a long line of sleeping birds, remained vacant for some time.

The British Tree Creeper *(Certhia familiaris brittanica)* was found by Rankin (1940) to roost in holes in the bark of introduced sequoias; a stuffed creeper placed in or near the hole was violently attacked by the bird returning to its sleeping place.

Discussion of Types of Territory

These types are not rigid categories. Types A, B and D merge into each other and often it is difficult to decide whether to place a certain bird in A or B, or another in B or D. In some instances a species may belong to one type in one region and elsewhere to another, as do the Eastern Goldfinch, birds of prey, Great Reed Warblers (Meylan, 1938), or even in the same pond some Great Crested Grebes may belong to type B and others to D. When birds are said to be "non-territorial," it usually means that they do not defend any considerable area, i.e., do not belong to types A or B, but it may be that they defend the nest-site and thus belong to type D.

With such an inclusive concept of territory, hardly any species is likely to be entirely "non-territorial," except perhaps parasitic species. The European Cuckoo does, however, hold territory, males and females separately. The Cowbird does not defend its breeding area, yet seems strongly attached to it. (Friedmann, 1929; Nice, 1937a, b; Lyon, 1935). Here seems to be a bird lacking in territorial behavior. Rand (1940) found no evidence of territoriality in Macgregor's Bird of Paradise nor did Davis (1940c) in the Monk Parakeet *(Myiopsitta monarcha)*, nor Tavistock (1930) in other Parakeets.

Many birds are attached to their wintering areas without showing any tendency to defend them. This has been shown experimentally by removing wintering birds to distant points; some return during the same season from remarkable distances (Pierce, 1925; Sumner and Cobb, 1928; Hilprecht, 1935; Simon, 1936; Wenkel, 1935; Mountfort, 1936; Sumner, 1938; Schifferli and Rüppell, 1939).

As yet little is known regarding flock territories. Lorenz refers to it in connection with Jackdaws (1931, 1935, 1938), Kirkman with Black-headed Gulls (1937), and Emlen with the California Quail (1939), while Yeates (1934) mentions it in connection with the Rook. Davis has given the most detailed description of this behavior in Anis and Guira (1940a, b).

Some birds return year after year to the same winter flocks, but show no defensive behavior nor exclusiveness (Price, 1933).

Territory in Other Vertebrates

Territory seems to be largely a vertebrate characteristic. Noble (1939) writes, "sexual territory is a direct consequence of the nest-building habit in vertebrates." There seems to be little information on the subject in invertebrates; Elton (1932) and Pickles (1938) describe territory in ants, and it may well be that other insects and Arthropods, especially Crustacea, have territory.

Among vertebrates many fishes and some lizards are strikingly territorial; with mammals the problem is more complicated. A brief survey will be given of this field, although of necessity it will be far from complete; yet some

knowledge of territory in other vertebrates is essential to our understanding of this mode of behavior in birds.

Fishes.—Many fishes are markedly territorial. As early as 1907 Cora Reeves described this behavior in the Rainbow Darter, large males of which "remain each within a restricted area which he guards and from which he drives other males. The width of these holdings does not usually exceed fifteen inches." The owner defends his "holding" by display and fighting. "When a male had once taken possession of a holding he received into it a succession of females and guarded it continuously against the intrusion of other males. In this way he not only secured to himself the successive females that visited his holding, but incidentally he guarded the eggs that had been deposited in it and prevented their being eaten by other males." So here territory brought the sexes together and protected the eggs.

Ter Pelkwyk and Tinbergen (1936) made a detailed study of breeding behavior in the Stickleback, describing the despotism of the male that first develops nuptial colors in an aquarium, the threatening signals of the males, the signals of the females, etc. In 1938 the same authors described the behavior of the Bitterling that lays its eggs in the gills of a mussel. "Just as in Sticklebacks and many birds we might speak here of a territory. The peculiarity of the Bitterling territory is that it moves with the mussel."

Noble (1938) gives many instances of territory in fishes. "In most territory-guarding fishes the males are conspicuously coloured and the females are conspicuous if they defend the nest or young. Exceptions occur in forms with poor vision and in some of large size. . . . The female reveals her state of gravidity: (a) In territory fish by approaching the territory-guarding male and by passively resisting his challenge. (b) In a few forms such as the salmon by actively engaging in nest building before the arrival of the male at the nest site. (c) In some school breeders by failure to flee or to gesture with her fins in the manner of a male, in others by driving the male or by vibrating the body."

In a study of the Jewel Fish, Noble and Curtis (1939), state the male usually claims territory first. "A territory-holding fish is dominant to those without territory but until nuptial bonds have been formed between members of a pair the male usually attacks only males, the female only females. After the bonds are formed each fish recognizes its mate by details of its color pattern, especially those on the head, and then the driving of other fish occurs regardless of sex."

Amphibians.—It is difficult to find evidence of territory in this class. Beebe (1925) mentions the female Smoky Jungle Frog *(Leptodactylus caliginosus)* in British Guiana as guarding her nest of foam in which the tadpoles developed; there are doubtless other more or less similar cases.

Reptiles.—In regard to snakes, Noble writes (1937), "Sex dichromatism is very rare in snakes and is correlated with the development of rivalry among the males of certain species." This is true of the European vipers, but "they

do not mark out definite territories which they defend against other males. At least aggregations of breeding vipers have been frequently seen."

I have been unable to get information regarding turtles.

Female alligators are said to guard their nests.

Many lizards defend territories. In regard to *Lacerta oxycephala,* Noble and Bradley (1933) write, "The male protects his domain from intruders. Bitter fighting ensues when males meet." Other species depend largely on bluffing with bright colors. "A female may remain with a male in this territory." In another article Noble (1934) tells us that bright colors have "been improved in the male line of many groups of lizards, for they serve as a warning that the territory is occupied and this in turn tends to prevent overcrowding. It is an advantage to the race for the males to be beautiful, for this scatters the individual territories of the males far and wide across the barrens."

With the chameleon, Evans (1936a) found that the "urge to acquire and to hold a certain restricted territory is very marked." When a male had been injected in winter with pituitary extract (Evans, 1935), he became brilliant green in color and dominated all the other chameleons which remained brown. "The other lizards kept their eyes on him, the females frequently gathering about him in a ring. . . . Observations made in the present study suggests that the mere flight of the female from the performing male quite probably signifies acceptance of the male and is therefore a very definite part of the complete courtship pattern."

Mammals.—Although a great many mammals have "home ranges," in general these do not seem to be defended with the vigor shown by many birds and fishes. Burt (1940) in writing of "territorial behavior" in wood mice, chipmunks, flying squirrels and shrews, says, "The small rodent that is ever in danger of being captured by one of its enemies must be thoroughly familiar with the area over which it travels." Territory is a necessity for food and shelter; it "is important in limiting the population in an area." Blair (1940) on the other hand, found that any given home range of the short-tailed shrew overlapped other ranges, so he believed that these animals "do not have 'territories' which they defend against other individuals of the same species and sex."

Groups of howler monkeys (Carpenter, 1934) "tend to occupy a definite and limited territory"; yet this "region may be shared with other groups. . . . Within their territories groups behave with reference to food and lodge trees." No combats between groups were seen, encounters being replaced by display which took the form of howls.

Territory has been recorded with Eskimo dog teams (Tinbergen, 1939a) and beavers (Bradt, 1938); the fur seal seems to display territorialism in an extreme form. Many examples of territory in mammals are given by Heape (1931).

The Bases and Functions of Territory

Territorial behavior occurs widely throughout the vertebrate series. *It is based primarily on a positive reaction to a particular place and a negative reaction to other individuals.* Or we may follow Craig (1918) in calling it an appetite for a place and an aversion towards other members of the species except the mate or mates.

Animals of very different kinds remain in the same place merely as a matter of habit. Banding has shown this to be true with many birds that return to their winter quarters under normal conditions and also when deported for experimental purposes. In his "Herd of Red Deer," Darling (1937) tells us: "Conservatism of habit, a factor of importance for the survival of species, tends to restrict movement to a particular area. . . . Choice is another reason for individuals or groups remaining on one area. Animals live in definite places because they like them. Familiarity with one piece of ground enables an animal to use it in the most advantageous manner for its comfort and well-being." We are familiar with the same phenomenon in ourselves, for we like to sit in the same place in classroom, church or public library, largely because, other things being equal, it is easier to do the same thing over again than to make new decisions, no matter how trivial.

Aversion towards other individuals has of late been the keynote of many studies on despotism, dominance and social hierarchy among birds, fishes and mammals (Schjelderup-Ebbe, 1922, 1935; Allee, 1936, 1938; Noble, 1939). Diebschlag (1941) clearly shows how in a flock of Domestic Pigeons the peck-order results from the endeavor of each bird to defend a certain area from other members of the flock. Wheeler (1939:254) considers dominance as equivalent to the "instinct of self-assertion. . . . If we regard dominance as an instinct it is certainly one so primitive and fundamental as to characterize all living substance and to be equivalent to self-preservation. Seneca wrote '*vivere militare est*,' which is paraphrased by Ortega y Gasset when he defines life as 'the struggle, the effort to be itself.' "

Conditioning to an area puts an animal into the best stimulus situation; the support from the familiarity of the environment enables it to be dominant there.

McCabe writes (1934) "in 'territorial' combat power is granted to the defender to win, always or nearly always, to the extent at least of defending his frontiers, whether it be by strength, by curious formalities of mimic warfare, or by the use of his voice, over an invading neighbor or wandering renegade." The "chief characteristic of territory," says Lorenz (1938), "is the fact that any individual will fight with very much more vigour if the combat is decided in his own territory." "A male on its own territory," writes Tinbergen (1939c: 57), "is undefeatable."

This "home-cage effect" is well known to people who work with animals; the "owner" of a cage, even if it has been there but a short time, is practi-

cally always victor over a new-comer. This has been shown for fishes (Ter Pelkwyk and Tinbergen, 1936), lizards (Evans, 1936a), voles (Ransom, 1934), white mice (Uhrich, 1938, Retzlaff, 1938), etc. Kirkman in his book on the Black-headed Gull *(Larus ridibundus)* (1937:61) writes:

> On two occasions I saw a chick—one not more than a few days old, the other in the half-down, half-feather stage—drive an adult bird away from its nest. That is all the more remarkable, for, outside the nest, the chick is a hunted creature, pecked by every adult it passes and fortunate if it escapes with its life. Yet, inside the nest, it opens its stubby wings, raises a small shrill voice, charges heroically, and the adult beats a retreat.

Dominance by those in possession is a commonplace observation in connection with domestic animals—chickens (Schjelderup-Ebbe, 1922, 1935), pigeons Craig, 1908; Noble, 1939), horses, cattle and dogs. It is not different with people—with children at play and in school, with sophomores and freshmen at college, with natives and strangers everywhere. Witness our proverbs—"Possession is nine points of the law," and "A man's house is his castle."

We have been considering territory in its widest sense as "a defended area." What about nesting and mating territories, Types A through D?

The defensive reaction towards outsiders is greatly increased in the case of a nesting or mating territory. Outsiders arousing antagonism may include all members of the species but possible mates, or to a lesser degree—other species, as with the Song Sparrow, Prothonotary Warbler (Walkinshaw, 1938a, 1939b), Mockingbird (Venables, 1940), Hummingbird, etc. Here it seems as if there were an hypertrophy of the territorial behavior. (The House Wren *(Troglodytes aedon)* is a striking example of this with its propensity to destroy eggs and young of hole-nesting species and even at times of birds with open nests—within or near its territory (Sherman, 1925).) The increase in pugnacity in these males seems to be related to the widespread protective instinct of many males for the mate, nest and young (Lorenz, 1935:302-306). Where the territory is a mating station only, the motive may be largely sexual jealousy. Where the female also protects the territory, be it Type A, B or D, her fighting reactions are intensified through her protective instinct towards the nest or young.

Many battles have been waged over the problem of the function of territory. Altum and Howard both believed firmly in the food value of territory, and on this point the latter was criticized by the Lacks (1933). In a great many cases there is no question of food value involved, but as Tinbergen (1939c) points out, "it is necessary to recognize that there are many species of Passerines to which the territory is necessary to provide a *certain amount* of food."

The possible limiting effect of territory on the number of birds nesting in a certain area has been questioned. The answer is yes and no. In many cases it does, the Song Sparrow and Great Crested Grebe being examples, the first typical, the second not. Many birds, like the Song Sparrow and House Wren (Kendeigh, 1941a) at first claim far more land than they

really need; under pressure of competition they decrease their holdings, *but not beyond a certain point.* In other cases territorial behavior adapts itself to circumstances, and the type changes, so that many more pairs are accommodated on a certain area than would otherwise be possible. Steinbacher (1938) counted 15 pairs of Kestrels *(Falco tinnunculus)* nesting in a small spruce woods where mice were abundant. According to Meylan (1938) the Great Reed Warbler *(Acrocephalus arundinaceus)* is territorial in most places, but in one lake in the Dombes as many as 50 pairs nest in one hectare of thick phragmites, three nests being found within 6 meters. With the White Stork in northern Africa when feeding grounds are restricted, new pairs are driven off, otherwise not (Bouet, 1938).

The chief function of territory is defense—defense of the individual, the pair, the nest and young. In many cases it also serves to bring the pair together and to strengthen the bond between them.

The protection afforded against despotism of other males, that results from the invincibility of the animal in his own territory, is one of the chief functions of all types of territory. Elsewhere I have said on the basis of my experience with the Song Sparrow: "I believe that the purpose of territory is primarily to prevent interference in family life" (1933:110), and again "Despotism in the nesting season is kept in bounds, as with Herons as described by Lorenz, by the factor of territory" (1939c).

The defense of territory may ensure to the animal food, shelter, and nesting materials. To ensure protection from interference with the orderly sequence of the nesting cycle, it is necessary that some species carry on all activities within the territory. In such cases the territory must provide a surplus of food for the pair and young in order to allow for adverse conditions.

As to the second function of some territories, Noble (1939) says "sexual territory . . . functions primarily to test sexual readiness of the opposite sex and to make possible the formation of sexual bonds." This would be true of types A and C and sometimes of B and D. In the latter types some birds take up territory after they are mated.

Territorialism is a significant characteristic of numerous vertebrates. "With animals, as with men," writes Craig (1921), "the cause of a quarrel is very commonly a coveted territory." Heape (1931), tracing territory through animals and human life, says:

> There can, I think be no question that territorial rights are established rights amongst the majority of species of animals. There can be no doubt that the desire for acquisition of a definite territorial area, the determination to hold it by fighting if necessary, and the recognition of individual as well as of tribal territorial rights by others, are dominant in all animals. In fact, it may be held that the recognition of territorial rights, one of the most significant attributes of civilization, was not evolved by man, but has been an inherent factor in the life history of all animals.

Despite the many available papers on the subject of territory, our knowledge is still incomplete. We know little about its occurrence in invertebrates,

amphibians, reptiles, and mammals. We do not know the *details* of its occurrence in birds: the signals of the males to each other and to the females, those of the females, the exact methods used by animals to obtain, proclaim and defend territory; the relationship of the female to the territory; despotism in wild birds and other animals; the minimum requirements of territories; and the possibility of a bird possessing an innate pattern of its territory. The scientific study of the social life of animals is recent and territory is an important element in the larger complex of such behavior.

Summary

A sketch is given of the history of the theory of territory in bird life. The first published notice appeared in 1622. Altum in 1868 was the true father of the theory, but his work passed unnoticed outside of Germany. Fifty years later—in 1920—Howard with his "Territory in Bird Life" brought the matter to the attention of the ornithological world.

Of the titles included in the accompanying bibliography, 34 appeared before the publication of this book and 344 since then.

Six types of territory are distinguished:

A. Mating, nesting and feeding ground for young. Example, Song Sparrow. Song in relation to territory and reserve supply of unmated birds are discussed here.

B. Mating and nesting, but not feeding ground. Example, Scarlet Finch.

C. Mating station only. Example, Gould's Manakin.

D. Restricted to narrow surroundings of nest. Example, Night Heron.

E. Winter territory. Example, Black-bellied Plover.

F. Roosting territory. Examples, Starling, Tree Creeper.

These types are not rigid, as some birds belong to one type in one locality and elsewhere to another.

With such a broad concept of territory, non-territorial birds are rare, the Cowbird and some Parakeets being our chief examples.

Many birds are attached to winter quarters without defending them.

Territory is found in many fishes and lizards and in some mammals.

Territorial behavior is based primarily on a positive reaction to most other individuals—an appetite for the former and an aversion for the latter. Conditioning to an area put an animal into the best stimulus situation; the support from the familiarity of the environment enables it to be dominant there.

In the case of the nesting territory, the male's fighting reactions are intensified through his instinct to protect his mate, nest and young.

Territory serves as a device for regulating despotism and a safeguard against interference in the nesting cycle. It also serves in many cases to bring the sexes together and to assist in the formation of sexual bonds.

Much research on territory is needed, i.e., on its occurrence in other forms besides birds and fishes, the techniques used for its maintenance, its minimum requirements, its relation to despotism, and on its place in the social behavior of animals.

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British Columbia Dragonflies (Odonata), with Notes on Distribution and Habits

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(With Descriptions of Two New Nymphs by E. M. Walker)

Introduction

Initial publications dealing with the Odonata of British Columbia were as follows:

Osburn R. C.—1905, The Odonata of British Columbia. Ent. News. **16**:184-196.

Currie, Rolla P.—1905, Dragonflies from the Kootenay District of British Columbia. Proc. Ent. Soc. Wash. **7**:16-20.

By perusal of the reference list, it will be noted that twenty-two years had passed since the appearance of these two papers and that of E. M. Walker in 1927. In this he included not only Osborn's and Currie's records but all additional ones to date; many of which were the result of his own collecting and some the work of the present writer. The author also included, under the latitude permitted by his title, a number of species that had been taken by himself or the present writer in the Alberta Rocky Mountains, and which consequently were deemed likely to occur also in British Columbia.

Since that time (1927) very considerable dragonfly collecting has been done in the Province by E. R. Buckell, in the territory centering upon the Okangan Valley, but wandering wide afield; by W. E. Ricker, in the Cultus Lake section; and by the writer, who, since 1934, has devoted his entire summer seasons to the work and has scoured the country as systematically as possible. This combined effort has resulted in not only a number of Walker's "probabilities" becoming facts, but the taking of some quite unexpected species and one entirely new: *Macromia rickeri*. So, in 1938, Buckell published his paper giving locality records for species taken by him or represented in the Dominion Laboratory at Vernon, and Walker a paper covering the work of Ricker and his associates in the Cultus Lake district.

But these later papers are primarily locality lists (with dates and some notes as to Ricker's species) and, dealing only with sections of the Province, limited in their scope. The present paper aims to cover British Columbian Odonata as a whole; to include notes on the habits of certain species and the association of species in cases of special interest: and thus continue north of the international border the work of Clarence H. Kennedy for the coastal States.

To achieve this, in the first instance, Walker's paper of 1927, with its admirable introduction, is used as a base, and the records of Buckell, Ricker

and the writer are incorporated to give the most comprehensive picture as to the distribution of the species. A map is supplied to further this end. This map, in the complexity of zonal and sub-zonal divisions on the southern border approximately follows that of R. M. Anderson in "Faunas of Canada." Farther north, where boreal forms only occur, conditions are less variable east and west, and the divisions are rather a matter of depicting geographical space than zonal change. And, in the extreme north, it is essential to consider the country as a whole, since collecting is necessarily limited to a few accessible points. The divisions of Vancouver Island in the neighbourhood of Parksville is in accordance with the writer's view that thereabouts a faunal change occurs. His own list demands it.

A peculiarity of the odonate fauna of British Columbia is a tendency in certain species of a number of genera to variability in size: notably *Lestes congener* and *disjunctus*, *Enallagma carunculatum*, *Somatochlora albicincta*, *Sympetrum decisum*, *pallipes* and *semicinctum*, and *Leucorrhinia hudsonica*. This is doubtless attributable to environment: for the mild coastal climate and the extremely varied topography of the country, combine to produce unusual conditions. Owing to these conditions, throughout the Province, and particularly upon the coast and in the Okangan Valley section, some species occur south and some north of their true range. But, where size is concerned, the writer considers altitude rather than latitude is the contributing factor. A good example in support of this argument is *Somatochlora albicincta*. The typical small form is northern or of high altitude. A medium-sized form occurs more southerly at lower altitudes. But the large form flies on the north shore of the Queen Charlotte Islands: northerly enough for its true range, but at sea level, within sight, smell and sound of the mighty rollers breaking upon Graham Island north beach (see plate).

My sincere thanks are due to my old friend E. M. Walker for his assistance these many years, and his special kindness in reading the typescript of this paper; and to E. R. Buckell and W. E. Ricker for specimens, information and willing aid at all times. If, as the writer believes will prove the case, no further general paper respecting the Odonata of British Columbia will be necessary for some decades, this will be due to the individual contributions of these his contemporary workers, now, supplemented by his own endeavours in the field, correlated into a convenient whole.

A concluding expression of thanks is reserved to Keith S. Hay, the companion on my caravan trips of 1936 and 1937, and whose assistance in scouting and in collecting specimens was of real worth.

Two large collections of mounted specimens have been built up in the course of my studies. One of these has been presented to The University of British Columbia, Vancouver, and the other to the Provincial Museum, Victoria. In addition, specimens have been given to The Canadian National Collection, Ottawa; The United States National Museum, Washington; The British Museum (Natural History) London, and individual collectors.

Foreword upon Dragonflies

While the collecting and study of dragonflies is, in the main, both interesting and exciting, it can likewise prove, upon occasion, irritating and disappointing. The irritation is usually due to inability to net some rare or greatly desired specimen that persistently keeps safely out of reach: for they have fine eyesight and the larger species are swift of wing. And the disappointment, consequent to having arrived at the hunting ground all expectant, to find that there is nothing flying.

The Sun's Influence

Those determined upon embracing Odonatology as a study must recognize one basic fact concerning these insects: viz., that they are sun worshipers. There are exceptions to this in a few twilight flyers and species of the genus *Aeschna* which will fly until dark after a sunny day. But, for active flight as to the great majority of dragonflies the sun must be shining in all its blazing glory: unobscured by even a filament of cloud. This does not mean that not a single damselfly or solitary dragonfly will be seen, but that of the many hundreds on the wing in the sun of yesterday but a corporal's guard remains: certainly not enough to make collecting other than a waste of time. Wind can be another annoyance; not that, given bright sunshine, dragonflies will not be on the wing, but that it tends to wild and rapid flight, with added difficulty in netting. However, better, infinitely better, wind with blazing sunshine, than the calmest day deficient as to sun.

Where do dragonflies conceal themselves at night and throughout the long cloudy day when, in spite of their voracious appetites, they prefer a state of starving quiescence? The obvious response would be: immobile upon the bushes, grasses, reeds, adjacent to the water: the same places, in fact, that they use for temporary rests when fly hunting in the sun. Such conclusion would be incorrect. Beat the bushes, grass, reeds upon a cloudy day around a lake teeming with dragonflies in yesterday's sun and the result is negative, save that a few damselflies may be secured. Yet, this we know, that should yesterday's sun blaze forth, those teeming hordes will be again in evidence. They are there: and the only conclusion is that they elect to hide back from the water in the higher bushes and, where available, in the trees.

Why do dragonflies prefer to rest and starve when the sun is not shining? Because the day is not warm enough? No, such midsummer days are frequently free from wind and warm almost to the point of humid heat. Because no small flies are on the wing and it is profitless to hunt? Again, no: the air may be full of flies on a day lacking bright sun, and not a dragonfly in sight. That they are sun worshipers, as already stated, seems the only solution; but I suggest that this is inspired by certain rays of the sun, which stir these insects to life. Once the sun arrives they take the air eagerly and very much awake. Until it comes they sleep. An exasperating fact to the Odontologist is that nectar feeders—insects instinctively associated with sunshine—will be flying, and apparently indifferent, on many a cloudy day when not a dragon-

fly is on the wing. Yes, he could make a fair catch of butterflies and an excellent collection of bees.

Dragonflies are one in that they must have sun, and that they feed upon flies, small and large, including their own kind; but in their individual characteristics the species are consistently different. Some pause in their foraging for flies, to rest high upon trees, some upon bushes, some prefer woodwork: palings, benches, jetties, floating logs or lumber, and some, again, the bare ground of road or path.

Oviposition

Egg laying also affords a diversity of methods: One species will select clear water, wiping an egg from the tip of her abdomen at intervals of say five or six feet; a second will favour spots mid the water plants, but a foot apart, and dip her ovipositor quickly three or four times at each such station; a third will grip the edge of a water-lily leaf and plunge her abdomen many times into the algae beneath; and a fourth will alight upon a reed stem, planting her eggs in it systematically, working lower and lower until she is totally submerged.

I have stated that the different genera and species of dragonflies have widely divergent methods of ovipositing, and I will now instance a specific example to which I gave close attention at Mud Lake, Forbes Landing, B. C. An *Aeschna* female (I think *canadensis*) settled near the end of a floating, bark-clad pole of some four or five inches in diameter. She stood upon the one inch and a half of dry surface, and immediately swung her abdomen overboard, stabbing eggs into the submerged bark. Next, by making a half turn, she dragged her abdomen over the dry surface and placed four or five eggs on the other side. What now? Would she fly away? No, she backed along the pole several inches and repeated the operation on either side. The following move brought her to a water-lily leaf, the edge of which touched the pole at that point, but, quite unconcerned, she dragged her abdomen over its surface until clear and continued her task. In twenty minutes she had worked her way along for possibly five feet, the water-lily leaf incident recurring several times in the process. Even in cases of careful observation it is dangerous to arrive at dogmatic conclusions, but the apparent inference in this instance would be that, once settled upon the pole, there was no coordination between her eyes and ovipositor. She depended solely upon the sense of touch. In spite of her wonderful eyes for looking forward and upward, is she quite blind as to the tip of her abdomen, three inches behind her? In such case, why did she elect to proceed backwards, when by heading in the direction of her course the impeding water-lily leaves would surely have been seen and the futile stabbing of these avoided? As to why there is no answer. It was the method instinct directed. In my opinion the purpose of the female appendages is to provide her with a delicate sense of touch in ovipositing. They tell her what she cannot see. In the aeschnines the styli would seem to serve the purpose of organs of touch, but whether in lieu of, or in addition to, the appendages is an open question.

Fertilization

To the female dragonfly a fine sense of touch at the end of her abdomen is imperative quite apart from egg laying. The unique copulatory embrace of the sexes, and the unlike position of the organs of fertilization demand that, once seized by the male, she take the initiative. Her abdomen must be swung upward, the genitalia be brought into juxtaposition and a precise connection made. Unquestionably the female appendages, and, in the case of *Aeschna* and Zygoptera females the styli, are the means to this end.

Judging by the behaviour of dragonflies, nature ordains a much more frequent fertilization of the females than in some of the other orders of insects: indeed, on occasion, copulation of the individual between her various bouts of egg laying may be observed. Such a requirement calls for lustful males, and, to do them justice, they take advantage of privilege to the point of license. I mean by this that not only do they pounce upon any female of their own species offering, but, where other species of the genus are flying—as is apt to be the case with *Aeschna* and *Sympetrum*—no nice discrimination is shown. Doubtless most of these efforts are incomplete and fruitless due to nature's provisions against cross-breeding, but knowledge of this propensity bids the student beware in accepting pairs as proof of identification.

Once the male appendages are snugly in position, he can hold his female firmly and for a long period. In the process of obtaining the requisite grip, however, his appendages may slip, and, should this happen but a short distance over the water, with dire consequences to the female. Unable to right herself in time, she falls on her back and drowns. The male instinct—so all sufficient to carry him through life—is quite unequal to such accidental tragedy. He flies away, apparently in ignorance of it, and unconcerned.

Flight

Dragonflies—I refer to the *Anisoptera*—possess three noticeable speeds, which may best be considered as *low*, *intermediate* and *high*. When hawking or seeking a mate, "low" is employed, and many species will pause entirely and, hovering, scan the horizon. When in "low" even such powerful insects as a *Macromia* on a roadway, *Cordulegaster* on its creek, or an *Aeschna* in a sunny glade, may be easily overtaken by the swing of the net, as they go by, when struck at from the rear.

"Intermediate" is used when the insect is travelling: *Macromia magnifica* crossing the river to take up a reach on the other side; *Cordulegaster dorsalis* crossing a lake to another creek. Momentarily they are not dallying for food, but are about their own business: "going places." At this speed they may still be netted, but it calls for perfect sighting and a rapid follow-through swing. It is something in the nature of an achievement, and, personally, I experience a feeling of jubilation when I net one of the speed artists in "intermediate."

"High" is the velocity of fright—the reserve power used to escape its natural enemies: barn swallows, kingbirds, cedar waxwings, yes, and the

collector's net. Strike at any of the species mentioned and miss, and instantly the insect goes from "low" to "high"—a high so rapid that the eye can scarcely follow. The black and gold *magnifica* becomes a blurred streak through the air! It is unquestionably *magnifica's* assurance of his own speed that nerves him to hawk leisurely along the banks of the Okanagan river, at Penticton—a bird sanctuary. He knows that they cannot catch him in "high."

Instinct

Instinct, which in the case of insects must serve for intelligence (and which, as J. Henri Fabre has shown is, in its various manifestations, wonderful beyond belief) is sometimes at fault. In the case of dragonflies, I witnessed recently an error of instinct past question, when I discovered a female *Sympetrum vicinum,* held and guided by the male, as is usual with this species, ovipositing in the dew-bespattered grass of a golf green. The wet moss around the edge of a lake is the correct depository for *vicinum* eggs, but the pair in question, having wandered far from the water, erred *instinctively* in accepting short wet grass as a substitute. I watched her performance for some ten minutes, and left her making a thorough job of it. An example from nature of "love's labour lost." Since this paragraph was first written I have not only seen other couples of *Sympetrum vicinum* ovipositing on golf greens, but, in Tahiti, on two occasions noted females of *Tramea limbata* wiping eggs from the tip of the abdomen into the sandy surface of the highroad.

The same species, *Sympetrum vicinum,* affords a good example of an individualistic trait that the insects positively force upon the collector's attention, though whether "curiosity" or "tameness" would best describe it, I cannot say. Dragonflies, generally speaking, are wary, and avoid the collector and his net. *Vicinum,* single males and females, and pairs flying tandem, will settle, on the sunny side of clothing, net and hands. I have had as many as eight of these beautiful little red dragonflies settled on me at one time. Turn slowly, however, to throw the insects into the shade, and all will depart. Whence comes this unusual tameness, or curiosity, in one particular species of *Sympetrum?*—this individual trait, contrary to the instinct of other members of the genus, and to the dragonfly clan as a whole? The question confronts us. We have not the remotest idea as to an answer.

Environment

Dragonflies are extremely local insects, showing strong preferences for this or that body of water: a large clear lake, or a small muddy one; a mountain stream, or a sluggish brook; a brave river, or a muskeg pot-hole. Two or three examples will best illustrate this trait. At Red Deer, Alberta, on July 1st, for three years in succession, I took the rare *Somatochlora hudsonica* at a small run-way of water near town, a hundred miles out of the insect's proper zone. At a tamarack swamp, a short distance from Red Deer, *Somatochlora franklini* occurred. True, in this instance, the tamarack swamp may be regarded as a Hudsonian zone island in a sea of Canadian zone, but the insects must observe the boundaries of their swamp and, so far as I could ascertain, they

did so. At Vancouver, the small blue and black damselflies *Enallagma boreale* may be taken all through the season at Beaver Lake, Stanley Park. If, on the other hand, I desired a series of *Enallagma carunculatum* I should not go to Beaver Lake, but to Lost Lagoon. Yet it is but ten minutes walk between the two lakes. The explanation is that the larger Lost Lagoon, with its broad reed beds, satisfies *carunculatum;* while the smaller, sheltered, water-lilied Beaver Lake meets the requirements of *boreale*. The same sort of thing occurs right through the dragonfly fauna.

This nice discrimination by dragonflies as to habitat adds greatly to the pleasure to be derived by the student of the order in the field. For, it follows, that if he knows the specific tastes of the individual species, he will, upon arriving at a strange body of water, first visualize its *possibilities*, and, with the netting of several specimens, speculate upon the *expectancy* of the place. Without devoting more space to the subject here, I suggest that, very broadly applied, a natural law—*the association of species under like environment*—lends its aid to the worker.

Sexual Maturity

Regarding the sexual maturity of dragonflies and damselflies, the experience of the collector would point to a distinct difference in this respect in most species as between the two sexes. In one hundred couples noted in copulation (various species) it would be safe to say that in over sixty per cent the males would be of adult coloration and the females not adult—many, indeed, quite teneral. Possibly thirty per cent would be represented by couples both individuals mature. And the remainder—a veritable sprinkling—where the male coloration indicated later emergence than the female. This would appear to lead to but one conclusion: that the males in this order are not physically fit to breed until truly adult, whereas the females are ready for fertilization by the male very shortly after transforming from the aquatic state.

Transformation

Dragonflies, upon emerging from the water of their nymphal state, do not (excepting a minor percentage of the stouter types) remain in the immediate vicinity; on the contrary safety lies in any place but there. In point of fact, until the insect is mature and ready to breed and lay its eggs, it has no need to be near water. A mountain top, or a sunny glade in the woods, is better in every way to come to strength, to catch flies and to play with its fellows. Even the stout-bodied dragonflies, as newly emerged tenerals, are, for a short time, at the mercy of birds; whereas the damselfly tenerals are devoured not only by birds and frogs, but by dragonflies, robber-flies, spiders and wasps. Barn swallows sometimes are particularly destructive to teneral damselflies; as a flock of them will patrol the lake-shore where the flies are emerging and virtually consume the entire flight.

The method of departure of teneral damselflies from the water's edge may be inspired by instinct, but it is certainly aided by kindly nature. Too weak

to fly against the breeze they flail the air frantically with their four narrow wings, (it might be likened to an autogyro) thus attaining elevation. The breeze does the rest.

In the active, aquatic, intermediate stage between egg and adult fly, these insects are unquestionably an important fish food; and, once on the wing, they are equally important (that is, valuable in the maintenance of nature's balance) in holding in check mosquitoes, midges, and other of the pestiferous host.

In Canada considerable study has been devoted to this order by a small number of workers—of whom the outstanding authority is Professor E. M. Walker of the University of Toronto—but the task is still incomplete both as to distribution of species and data respecting habits: while, as to full life histories, these are for the greater part unknown.

Suborder **Zygoptera**

LESTIDAE

LESTES CONGENER Hagen

The eastern description for this insect "a rather small blackish brown species," while true for Alberta specimens, is not so for the large *congener* of British Columbia.

In this Province it appears to be very local, but the fact that it is the last of the genus to emerge, restricting collection to August into September, may explain the somewaht scanty records. Walker (1927) gives localities in the Okanagan district and Vancouver Island. I can extend the mainland distribution eastward to Crawford Bay, West Kootenay, August 10th 1928; and eastward to Hope and Harrison Bay, dates August 1st-12th, 1936. At Hope I took specimens both at the sloughs on Little Mountain, and at Texas Lake. In Harrison Bay district, it was flying up Elbow Lake creek to the headwaters, where *Octogomphus specularis* and *Cordulegaster dorsalis* also occurred. Specimens from this locality, sent to Walker, drew the comment: "larger than any I have seen."

The single teneral taken at Sooke, June 13th, (and that I feel sure was premature) was the only locality record for *congener* on my three months Vancouver Island trip, 1937. Walker (1927) records it as emerging in the Nanaimo district August 7th-13th, by which time I was many miles north at Forbes Landing, and, possibly, out of its range.

Further distribution: In 1938 I took *congener* at the following localities: Golden, August 14th, emerging (small size), Kamloops (river reeds and Lac le Jeune) August 19th and 24th; Jesmond, August 29th, pairs and singles. Buckell (1938) gives no less than 33 stations, from Prince George in the north to Osoyoos on the international border, from Similkameen in the west to points near the eastern boundary, which serves to disprove my original impression as to the insect's scarcity.

In 1940, I took a single teneral male, the small northern form, at Tête Jaune, August 10th. I also received a long series from Dawson Creek, Peace River District, without dates.

Flight period: July 10th to November 10th.

Map areas: 1, 4, 5, 6, 7, 8, 10 and 14.*

Lestes unguiculatus Hagen

As in Alberta, this species is on the wing well ahead of *Lestes congener:* Walker (1927) states as early as June 12th. My mainland records, working eastward, are: Chilliwack, July 23rd; Cultus Lake, July 6th; July 26th, and Crawford Bay, West Kootenay, August 17th. At none of these was it plentiful.

My Vancouver Island trip, 1937, provided but two locality records for this species: Sooke, "emerging in numbers," June 13th; Florence Lake, a mature male, July 2nd, and "fairly common, but scarcely adult," July 5th. Walker (1927) also supplies the Nanaimo and Saanich districts, but, while I stayed in the former from July 8th to 16th, I saw nothing of the species: probably I had moved north ahead of its flight there.

Further distribution: In 1938, July 18th-19th, I found this species fairly plentiful, and of large size, at a dry slough at the south end of the Okanagan river, Penticton district. Walker (1927) gives mainland records: Armstrong, and Okanagan Landing; and (1938) Chaperon Lake, August 26th. Buckell (1938) contributes: Canal Flats, Hat Creek, Osoyoos, Premier Lake, Princeton and Wasa. J. Wynne sent me specimens from Enderby, August 4th.

It is by far the most local species of the genus in British Columbia.

Flight period: June 12th to August 24th.

Map areas: 1, 4, 5, 7 and 8.

Lestes dryas Kirby (*L. uncatus* Kirby)

The flight period of this species is two weeks earlier than that of *unguiculatus*. I took it at Crawford Bay, West Kootenay, mid-August 1928: and my more recent mainland records are Cultus Lake, (plentiful) July 2nd-18th, 1936; Chilliwack, July 23rd; Hope (Silver Creek slough, Little Mountain, Hope-Princeton trail) July 26th-August 2nd.

On Vancouver Island (my trip of 1937) I found this species in the south at Sooke, "common, adult and in cop.," as early as June 7th. This was at the reedy pool where *Ischnura erratica, cervula* and *perparva* were flying with *Sym. illotum* and *Somatochlora semicircularis*. At the same pool, but not until June 13th, I took newly emerged tenerals of *unguiculatus* and a single teneral of *congener*. The last mentioned was probably a 'freak' emergence, as the insect is usually well subsequent to *disjunctus* in making its appearance.

* See map on page 556.

My additional records were: Florence Lake, July 1st; Nanaimo district: Departure Bay, plentiful, July 8th.

Further distribution: In 1938 I took *dryas* at Kaslo, June 21st; Penticton (large size) July 17th; Revelstoke, 4,500 ft., August 3rd, Kamloops, August 19th. Walker (1927) adds Wellington and Gabriola Is. to the Vancouver Island list, and (1938) Chaperon Lake, to the mainland habitats. Buckell (1938) contributes 28 localities, with northern points, Canim Lake, Chilcotin and Horsefly.

On my trip of 1940, Prince Rupert to the Alberta border, I took but two specimens of this species: at Vanderhoof, July 8th, an adult male, and at Mount Robson, Aug. 6th, a male.

Flight period: June 7th to Sept. 6th.

Map areas: 1, 4, 5, 6, 7, 8, 9 and 10. Mrs. Gloyd's Synopsis (1939) gives one record from Alaska.

LESTES DISJUNCTUS Selys

This is the common *Lestes* of British Columbia: one of those things, like *Libellula quadrimaculata*, ever with the collector. On the Queen Charlotte Islands, Massett district, 1935, I found emerging from lakes, sloughs and muskeg pot-holes July 20th on; and by July 26th adult and in cop. This is roughly three weeks later than the general emergence at Beaver Lake, Stanley Park, Vancouver, which occurred in 1935 on July 27th. Walker (1927) gives dates of flight to August 16th, but remarks: "they doubtless occur later than this." My records indicate that at Vancouver as late as September 2nd they are "common, in cop.," and that the flight continues in reduced numbers to September 24th.

This species emerges on Vancouver Island, so my trip of 1937 would serve to show, at approximately the same time as on the mainland. My notes supply records as follows: Thetis Lake, a teneral male, June 24th; Florence Lake, a teneral male, July 2nd, and several still teneral July 5th. Wellington Lakes (pot-hole), "large specimens, adult and in cop.," July 14th; Courtenay, July 20th; and Forbes Landing, July 26-August 18th. A comparison with the data given respecting *L. congener*, *dryas* and *unguiculatus* makes clear that while *disjunctus* is later in getting on the wing than the two last mentioned, it is the only species of the four *Lestes* that I have taken north of the Nanaimo district. Further collecting may disprove this, but it must stand for the present. In a country of mountains, hills, lakes, rivers and coniferous trees —and such is Vancouver Island—it is difficult to draw an arbitrary line and to state that *there* a zonal change occurs; but I feel that a change does come into effect as to the odonate fauna not far north of Nanaimo, and I now recollect that no Arbutus trees were noted by me north of Parksville. Provisionally, then, I draw a dividing line at that point. Shall we find *Pachydiplax longipennis* and *Erythemis s. collocata* north of it, or *Somatochlora walshii* and *minor* to the south?

Further distribution: In 1938 *disjunctus* was flying at the following: Kaslo, June 24th; Vernon (Deep Lake) July 26th; Enderby, July 31st; Revelstoke, August 4th; Field, August 10th; Golden, August 14th; Kamloops (river reeds and Lac le Jeune) August 19th-24th; and Clinton, August 28th; and, in 1936: Hope, Hatzic Lake and Harrison Bay, July 26th-August 9th. The species is common everywhere, but I will show extension of its range by selections from other lists. Walker (1927) Prince Rupert, Okanagan Landing, Nelson, Metlakatla, Peachland; and, (1938) Chaperon Lake, Chilliwack and Cultus Lake. Buckell (1938) gives 46 localities, ranging as far north as Prince George (Summit Lake) and Palling, i.e., north of 54″. At Atlin, 60″ north, *disjunctus* emerged July 17th and by July 22nd they were plentiful, flying in cop. Two or three survivors seen as late as August 28th. It was the only species of the genus at that latitude.

On my trip of 1940, Prince Rupert to the Alberta border, I found *disjunctus* at Vanderhoof, July 8th, fairly common, adults and tenerals; McBride, July 12th; Mount Robson, Aug. 4th, and Tête Jaune, August 8th.

Flight period: June 20th to September 24th.

Map areas: 1-13. Mrs. Gloyd's Synopsis (1939) provides a number of records for Alaska.

Coenagriidae

Argia vivida Hagen

There are but two locality records for *vivida* in British Columbia: a single specimen taken by Osburn at Glacier many years ago, and a long series by Buckell at Field.

In 1938 I spent August 6th to 13th at Field, but whether I was too late or the somewhat inclement weather was against me, I certainly failed to find *vivida*.

Walker (1927) inclines to the view that the presence of this species in numbers at Banff, Alberta, would seem to associate it with the hot springs. Buckell's Field captures would fail to support such argument, for their creek —the local people take rather special pride in it, and urged, nay insisted, that I drink some—analyses 100% pure spring water.

Flight period: June 12th to August 27th.

Map areas: 7 and 8.

Note: Field is a railway divisional point, and the thought occurs that Buckell's specimens may have come, not from the creek, but some drainage ditch from the roundhouse, the temperature of which was artificially raised by hot waste or contiguity to hot ash dumps.

Argia emma Kennedy

At Cultus Lake in 1936 this species—previously taken there by Ricker—was emerging in the afternoon of June 18th, but none reached adult colora-

tion until June 25th, when numbers were observed in cop. The insect was very plentiful: the breeding water undoubtedly being Sweltzer creek which also produces *Octogomphus specularis* and *Ophiogomphus occidentis*.

On July 31st 1936, camped on the Coquihalla River, Hope, *A. emma* was again located, the breeding place here being the clear water creek draining Kawakawa Lake into the Coquihalla. Hopes ran high; If *emma* associated with rare gomphines on Sweltzer creek, why not on Kawakawa creek? But, on August 7th I moved eastward to Hatzic Lake, leaving *emma* at Kawakawa creek on August 6th "numerous as ever." Ricker, consulted, states the insect flies at Cultus Lake until August 26th.

Distribution: In 1938 I found this species common at Christina Lake, July 3rd-15th; and on the Okanagan river, Penticton, July 16th-22nd. Walker (1927) recorded Penticton and also gave Oliver, with date July 22nd. His (1938) list recorded many specimens taken at Cultus Lake by Ricker, the discoverer of the species there. Buckell (1938) contributes two additional localities: Lillooet and Mabel Lake. These are approximately 75 miles farther north than Penticton.

At the south end of the Okanagan river the insects were ovipositing; and I would see as many as six couples, side by side, within a space of several inches: the males attached in their perpendicular poise so well illustrated by Kennedy (1915, p. 281). A most unusual sight, and not without a touch of the humorous!

Flight period: June 18th to August 26th.

Map areas: 4, 5, and 6.

Amphiagrion abbreviatum Selys

This is the species recorded by Walker (1927) as *A. saucium* (Burm.), but he commented upon the fact that it was off-type in size and robustness. In view of Mrs. Gloyd's research respecting *Amphiagrion*, the British Columbian representative must now be classified as above.

Walker gives but two locality records in the Province: Peachland (mainland interior) and Victoria (Vancouver Island) I can add five more: Vancouver, reedy pond adjoining the reservoir, Stanley Park, May 25th-30th 1935; Cultus Lake, slough near Indian village, a good series, July 2nd-6th 1936; and Florence Lake district, Vancouver Island, June 30th and July 2nd 1937, 2 tenerals. This one locality record on the Island, as the result of my three months' intensive collecting that year, would indicate but scant distribution. It likes shallow, sun-lit, hard-bottomed, reedy marsh or runway, as favored by *Ischnura erratica*, and this particular type of breeding place is by no means common. In 1938 I took 2 males at Kaslo, June 24th, and several at Penticton, July 15th.

Buckell (1938) adds six localities: Canoe, Hat Creek, Kaleden, Lumby, Salmon Arm and Vernon.

Flight period: May 16th to August 1st.

Map areas: 1, 3, 4, 5, 6, and 7.

Nehalennia irene Hagen

In this, the most delicate of our *Zygoptera,* the female form (though slightly stouter) closely resembles the male. A timid little insect, it keeps well down in the reeds; and I have found that sweeping with the net is more effective than searching for individuals.

The coastal area, with its lower altitude, appears unsuitable to *irene,* nor has it been taken on Vancouver Island.

Walker (1927) gives records of Nelson and Revelstoke; and, in the latter district, I took a long series at Williamson's Lake, August 2nd, 1938: males being the more plentiful. Buckell (1937) supplies additional localities: Chase, Salmon Arm and Prince George (Summit Lake).

In 1940, between Prince Rupert and the Alberta border, I found this species only at Vanderhoof; Buckell's Summit Lake record stands, therefore, as the most northerly habitat.

Flight period: May 10th to August 2nd.

Map areas: 5, 6, 7, and 10.

Coenagrion resolutum (Hagen)

The only southern record in the Province is that of Walker at Nelson, July 19th-21st. He also gives the same dates for Revelstoke. Buckell's localities range northward from Bridge Lake, Jesmond, Chilcotin, Stanley to Prince George.

On my trip of 1939, 60″ north, I found this species flying at muskeg pools July 6th with *Enallagma boreale* and *cyathigerum; Somatochlora hudsonica, albicincta* and *septentrionalis; Aeschna eremita* and *coerulea septentrionalis.* The total series of 11 males and but 2 females of *resolutum* would indicate that the insect was by no means plentiful. My latest date was July 22nd. In Alberta, my records show, *C. resolutum* was one of the three first species to appear (end of May), *Leucorrhinia borealis* and *hudsonica* being the others.

In 1940, working the territory between Prince Rupert and the Alberta border, lat. 53″ to 55″ N., I found this species plentiful at Smithers, June 22nd; Burns Lake, June 29th; Vanderhoof, July 8th; and (now getting scarce) McBride, July 12th.

In a long series, specimens will be found with the antehumeral bands divided into an anterior stripe and a posterior spot, as in the case of *C. interrogatum*.

Flight period: June 14th to August 18th.

Map areas: 4, 6, 7, 9, 10 and 13. Alaska, 3 records (Gloyd 1939).

Enallagma clausum Morse

Up to the date of Walker's 1927 list, the only record of *clausum* in British Columbia was his own, at Penticton, July 28th, 29th, 1926. Since then Buckell (1938) has published captures at Osoyoos; and still more recently (an unpublished list for 1937) he adds Jesmond and Quesnel, in the Cariboo district.

At Penticton, July 15th to 21st 1938, I took a long series of *clausum*, where it was flying with all the other species of the genus in the Province, excepting *hageni; Amphiagrion abbreviatum, Argia emma, Lestes dryas* and *unguiculatus, Ischnura cervula* and *perparva*.

As Walker points out, *clausum* in B.C. in general appearance (size and colour pattern) resembles *boreale* and *cyathigerum*. Its female, however, differs from theirs in that segment 8 is wholly blue: this is most helpful in the field.

Flight period: July 2nd to August 22nd.

Map areas: 4, 5 and 10.

Enallagma boreale Selys

This insect—*E. calverti* Morse of my Alberta lists—shares with *Ischnura cervula* the distinction of being on the wing longer than any other species, *Zygoptera* or *Anisoptera*, in British Columbia. It emerges as early as April 29th at Stanley Park, Vancouver, and, brood succeeding brood, it may be taken there to mid-October.

In the Massett district, Queen Charlotte Islands, July 18th-30th, *boreale* was flying at pools, pot-holes and lakes of the upland muskeg: being the only species of the genus I took there.

In Alberta, to the best of my recollection, this species and *E. cyathigerum* flew together, but in British Columbia my experience serves to confirm the statement of Walker (1927) that this is unusual: Texas Lake, Hope, August 3rd 1936, provided an exception, and Penticton was another.

Owing to the likeness of this species to *cyathigerum* on the wing, at every piece of water visited many of the little blue damselflies must be netted and examined under a magnifying glass to determine which of them was present, or, though this be improbable, both. My Vancouver Island trip, 1937, gave records for *boreale* as follows: Sooke, (*Ischnura erratica's* reedy pool) June 7th; Nanaimo district: Departure Bay, July 8th and Newcastle Island, July

16th. Courtenay, July 20th; Forbes Landing district: Upper Campbell Lake (flying on lake shore) August 11th.

A comparison of this list with *cyathigerum's* localities is interesting, for though the territory covered is the same, the actual breeding place is in every case different. Nor is solution of the riddle simple, such as one preferring large bodies of water, the other small: for in each list are instances of both, and also those of great similarity. The thing is the antithesis of the case of *Ischnura cervula* and *perparva*—the inseparables!

Distribution mainland (selected): Walker (1927) Prince Rupert, Penticton, Revelstoke, Nelson; and (1938) Chaperon Lake. My 1936 records include: Hope and Harrison Bay; and those of 1938, Kaslo, Vernon, Field etc. Buckell (1938) gives 37 localities, and, subsequent to that list, 3 additional. The extent of his range is much as stated under *Lestes congener*.

In 1939, at Atlin (60″ north) I took a short series of *boreale* July 12th to August 28th, but it was scarcer than *cyathigerum*, the other truly northern species of the genus.

During my trip of 1940, I took this common species right across the Province: Terrace, June 17th; Smithers, June 22nd; Burns Lake, June 29th; McBride, July 12th; Tête Jaune, Aug. 8th; Mount Robson, Aug. 4th.

Flight period: (continuous emergence) April 29th to October 10th.

Map areas: 1-13. See also Mrs. Gloyd's Synopsis (1939) for records in Alaska.

Enallagma cyathigerum (Charp.)

Walker (1927) gives a number of records, covering a wide range. I will select from mine those that best serve to contribute new territory: mainland, Lower Fraser Valley section: Cultus Lake, July 9th; Chilliwack, July 17th; Hope (Silver Creek) July 26th; Hope (Texas Lake) August 3rd; Harrison Bay (Squawcum Lake) August 15th-19th, flying in hundreds, in cop. Vancouver Island: (northerly) Forbes Landing (Mud Lake) August 9th; Courtenay (Northey's Lake) August 13th.

My Vancouver Island trip, 1937, provided locality records as follows: Sooke, (Young's Lake) mature and in cop., June 12th; Thetis Lake, June 14th; Florence Lake, June 30th-July 4th; Nanaimo district: Wellington Lakes; Forbes Landing: Mud Lake and Lower Campbell Lake, July 26th-August 18th. Courtenay, "Forbidden Plateau," (3200 feet) August 26th.

In 1938 I took this species: Kaslo, Crawford Bay, Christina Lake, Penticton, Vernon, Golden, Kamloops and Clinton, in the Cariboo, where it was very common. Walker (1927) records: Atlin, Chilcotin, Prince Rupert, Okanagan Landing, Nelson, Cranbrook, Bear Lake, Peachland, and, (1938) gives additional stations: Rosedale and Chaperon L. Buckell (1938) contributes 36 locations, north to Prince George.

On my trip of 1939 to Atlin (60″ north) I found this species fairly common July 6th, and it was at the height of its flight July 9th to July 19th. Frost occurred Aug. 3rd and Aug. 11th, but I netted single survivors August 27th and 29th.

In 1940, on my trip between Prince Rupert and the Alberta border, I netted this species at: Terrace, June 18th; Smithers, June 22nd; Burns Lake, June 30th, and, Vanderhoof, July 8th, but none eastward of that point.

Usually in western Canada the colour markings of this species and *E. boreale* are identical, therefore the specimens taken by me of *cyathigerum* at Terrace (Lakelse Lake) are worthy of special mention. The dorsum of the abdomen was heavily marked, reminding one superficially of *E. carunculatum*. Walker confirmed my identification, and stated that he had never seen specimens of *cyathigerum* like those sent to him.

Flight period: May 17th to October 8th.

Map areas: 1-11, -3 and 14. See also Mrs. Gloyd's Synopsis for records in Alaska.

ENALLAGMA HAGENI (Walsh)

There was no good reason why this species should not occur northerly in British Columbia, for I had taken it in the adjoining Province of Alberta in 1918, at Red Deer; but the fact remains that it was unrecorded until 1937, when Buckell took 8 males at Stanley, in the Barkerville district, July 9th. The two points mentioned are of about the same latitude: north of 52″.

Flight period: (based upon Prairie records) Mid-June to end of July.

Map areas: 10.

ENALLAGMA EBRIUM (Hagen)

The two records given by Walker (1927) are in the Okanagan district, Penticton and Oliver, June-July, and I took it at Enderby July 31st 1938. Buckell contributes several more localities in the Sonoran-dry Transition section: Vernon, Falkland and Kamloops. Farther north, he records Bridge Lake and Prince George. Ricker found it at Chaperon Lake, July 27th 1934. *Ebrium* also ranges eastward into the Kootenay Lake section. I netted a long series at Crawford Bay, June 28th 1938, and Buckell supplies Boswell and Wasa in that area.

At Penticton, July 15th-22nd 1938, I took it flying with *carunculatum, boreale, cyathigerum* and *clausum*, but at Crawford Bay (Fraser's Lake) and Enderby the first mentioned only was present.

My trip of 1940, Prince Rupert to the Alberta border, added one northern habitat to that supplied by Buckell at Prince George, viz, Burns Lake, July 4th. These are both north of Lat. 54″.

Flight period: June 8th to September 3rd.

Map areas: 5, 7, 8 and 10.

ENALLAGMA CARUNCULATUM Morse

In this Province, where the tendency is to oversized insects in a number of genera of *Odonata,* this species provides, in certain localities, the sole exception that I have noted of an undersized form. At Lost Lagoon, Vancouver, the insects are very uniform, length 34-36 mm., and this I regard as normal. Specimens of similar type have been taken by me on the mainland: Lulu Island, August 21st; Chilliwack, July 15th; Hope (Texas Lake) August 3rd; Hatzic Lake, August 8th; Crawford Bay, West Kootenay, August 19th, and Nelson, July 27th-August 28th.

My localities for the smaller form are: Campbell River, Vancouver Island --the most northern record for the species—August 6th-7th; and, on the mainland, Hope (Kawakawa Lake creek) August 4th. The Hope specimens are not only short in length, but slim bodied; in fact, less robust than *Ischnura erratica.*

On Vancouver Island my three months' trip, 1937, only resulted in four additional records: Thetis Lake, emerging, June 22nd; Florence Lake, emerging, July 5th; Nanaimo district: Wellington Lakes, adult—common, July 14th; and Forbes Landing (Mirror Lake) 2 males.

Further distribution: In 1938 I took this species, Kaslo, June 19th; Christina Lake, July 4th; Penticton, July 15th; Vernon, July 27th; Enderby, July 31st and Revelstoke (valley) August 4th. Walker (1927) gives additional locations: Okanagan Landing and Nelson, and (1938) Chaperon Lake. Buckell (1938) contributes: Bridge Lake, Canim Lake, Douglas Lake, Mabel Lake, Nakusp, Oliver, Osoyoos, Salmon Arm and Sugar Lake. The species is clearly of wide distribution in the Province, but less so than *boreale* and *cyathigerum.*

My trip of 1940 provided an interesting record for *carunculatum* at Burns Lake: a teneral male, June 30th, and further tenerals and adults July 4th. The specimens were taken on a road, near a small creek bed, now reduced to a few stagnant pools. Walker (1927) places this species in the General Austral Fauna, so Burns Lake, north of 54″, must be regarded as distinctly boreal for the insect's true range.

Flight period: June 4th to September 29th.

Map areas: 1-7, 10.

ISCHNURA CERVULA Selys

Kennedy (1915), writing of this species and *I. perparva,* states: "wherever I have found one, the other . . . has always been found." This has been my experience almost invariably in British Columbia, say from May 24th to August 24th: *perparva's* approximate flight period. But *cervula* is the rival of *Enallagma boreale* as to the length of its season: my records dating from May 7th to October 25th.

In the field mature *cervula* males are instantly recognized by the spread of the wings when settled and the four blue spots on the dorsum of the thorax. The homoeochromatic female appears the most common, differing from the male in that only segment 8 is light blue, instead of segments 8 and 9.

On my Vancouver Island trip, 1937, the records were: Sooke, June 7th; Thetis Lake, June 14th; Florence Lake, June 30th-July 4th; Nanaimo district: Departure Bay, July 8th; Wellington Lakes, July 14th; Newcastle Island, July 16th; and Forbes Landing, July 26-August 18th. The last mentioned locality is the most northward on the Island, but I do not doubt that it extends into the highwayless northern section.

Distribution mainland: during 1935 and 1936 I took *cervula:* Vancouver district, Cloverdale, Cultus Lake, Chilliwack, Hope district, Hatzic Lake, and 1938, Kaslo, Crawford Bay, Christina Lake, Penticton, Vernon, Enderby, Revelstoke. The records given by Walker (1927 & 1938) relate to much the same territory. Buckell (1938) extends the range northward with the following localities: Bridge Lake, Redstone, and, notably, Quesnel, situated on 53″.

Flight period: (continuous emergence) May 7th to October 25th.
Map areas: 1-7, 10.

Ischnura perparva Selys

Males of this species, besides being smaller than *cervula,* may also be distinguished in the field by the striped dorsum of the thorax and the light breaks between the abdominal segments. The orange and black females are easy to detect; whole those of the pruinose from mope among the grasses like little ghosts.

Walker (1927) gives southern Vancouver Island records, and but one on the mainland: Penticton. Avoiding his territory, I select, mainland: Vancouver May 24th-August 24th; Lulu Island, August 21st; Cultus Lake, July 1st; Chilliwack, July 17th; Hope, July 28th; Hatzic Lake, August 8th; Harrison Bay, August 15th. Vancouver Island: Campbell River, August 6th; Forbes Landing, August 9th; Courtenay, August 14th.

On Vancouver Island, 1937, my locality records and dates were—as might be expected—precisely the same as those for *I. cervula,* and repetition is unnecessary.

Further distribution, mainland: Enderby, Revelstoke valley (F. C. W.); Buckell (1938) Bridge Lake, Kaleden, Lumby, Oliver, Osoyoos, Peachland, Robson, Similkameen, Vaseaux Lake. Of these Bridge Lake alone ranks as northern. Further, it must be admitted, in spite of what was said under *I. cervula* as to the association in the field of the two species, that a long list of actual records on the mainland fails to substantiate the statement. It would be truer to state: where *perparva* is, there also *cervula* will be found.

Flight period: May 16th to September 9th.

Map areas: 1-6, 10.

Ischnura erratica Calvert

This, a somewhat rare species, was located by me near Cultus Lake—precisely, a shallow reedy runway close to the Indian Village—on July 2nd 1936: Ricker had taken a male a day or two previously at what he calls "Lost Slough" and he had a previous record August 4th 1934. On the date given I took a pair in cop.; and single males on July 6th and July 9th.

The runway was quite shallow, possibly thirty feet across and one hundred feet long. It was drying up rapidly. At this insignificant piece of water, on July 2nd were flying, beside *Ischnura erratica, cervula* and *perparva; Lestes dryas* (common), *disjunctus* and *unguiculatus; Amphiagrion abbreviatum* (fairly common); *Libellula quadrimaculata* and *lydia;* two males *Somatochlora semicircularis* (both netted) and *Sympetra: pallipes* et al.

On the water the *erratica* male cannot be confused with *cervula* or *perparva,* for while alike as to general appearance (particularly the latter, since it also has the light rings between the segments), it is distinctly larger; and the light blue patch near the end of the abdomen, occupying as it does segments 9, 8 and the apical half of 7, instantly catches the eye. The female taken was the small pruinose form.

My only record for this species on Vancouver Island, 1937, was in the extreme south at Sooke, June 7th-9th. The breeding place was very similar to that in the Cultus Lake district and, excepting for the absence of *A. abbreviatum,* its associates were the same. I took a series of males and one homoeochromatic female. The latter, while slightly shorter and stouter, is otherwise very like the male, even to the light blue patch intruding into segment 7. She is easily identified on the water. I conclude that *erratica's* rarity is due to strict requirements in its breeding place: whereas the commoner *I. cervula* and *perparva* appear satisfied with anything from a pool to a large lake, from a reedy marsh to a brook.

Further distribution: Walker (1927) records four localities, by various collectors, all on Vancouver Island: Ucluelet, July 19th; Sahtlam, May 11th and 15th; Victoria, May 10th and June 2nd; and Langford Lake, July 30th.

Flight period: May 10th to August 4th.

Map areas: 1 and 4.

Suborder **Anisoptera**

Cordulegasteridae

Cordulegaster dorsalis Hagen

This is the largest dragonfly in the Province, females having a length up to 87 mm., which exceeds our *Anax junius* of the same sex, though the latter species has a slight advantage in wing spread: 108 mm. as against 110 mm. Needham (1929) states that the wings are hyaline, and Kennedy, though giving the colour pattern, makes no mention of the wings. In females the costa is stained yellow to the wing tip.

I have had quite exceptional opportunity of observing *dorsalis*, since it flies on the small creek which feeds and empties Beaver Lake, Stanley Park, Vancouver. Here it is at sea level, in fact, close to salt water. The flight up and down the creek is as described so admirably by Kennedy (1917). In August 1936 I discovered *dorsalis*, in numbers, on Elbow Lake creek, Harrison Bay district, flying with *Octogomphus specularis*. The creek grade is followed by an abandoned logging railway, which crosses it a number of times and affords the collector close access to the water. Bushes encroach upon the roadbed on either side. Under such conditions the insects, both male and female, leave the creek at obstructions, or for sunshine, and fly up and down between the bushes: I caught a female and a number of males on bridges and flying over the ties, where the same somewhat slow but very direct flight is observed. If frightened, the insect can fly with incredible speed.

Kennedy states that the female he watched ovipositing "usually faced the centre of the stream"; and this always struck me as strange on her part, since to keep in the right depth of water, she must obviously follow the contour of the shore line. Kennedy's female was I think the exception to the general rule: certainly those noted by me faced the bank. The last one observed, August 21st, worked her way along upstream in the shade under a log bridge, and having used her spade every five inches or so, she finished her task by swinging over deeper water (possibly ten inches) and washing off the tip of her abdomen several times.

On August 14th a pair were observed flying in cop. over the water at a small dam near the headwaters of Elbow creek. They turned and went back toward Elbow Lake, some hundred yards distant. Both sexes will rest on bushes along the railroad track, on trees over the water, and (one instance) on the face of rock dropping perpendicularly to the creek.

I have taken *dorsalis* from June 21st at Vancouver to August 21st at Elbow creek. But the former were past the teneral stage, and the latter were by no means over, so, to estimate the flight period as from mid-June to the end of August should be within the facts.

In spite of the scant published records for *dorsalis* in British Columbia, I am convinced that it is one of the most widely distributed coastal species from California to Alaska (see Kennedy 1917, Gloyd 1939). On Vancouver Island, 1937, my records were: Florence Lake, June 30th; Goldstream, July 4th; Departure Bay, July 8th; Wellington Lakes, July 12th; Newcastle Island, July 16th; and Forbes Landing, every creek in the district, July 25th to August 18th.

This species will wander from its creek; and I have taken them hawking in an orchard, flying on lake shores and on sunny roads. Near the largest of the Wellington Lakes—far from any creek—I observed two females hawking over a road. One was seized by a male and I netted the pair in their heavy flight, date July 12th. Their requirements as to a creek are very broad—any-

thing from a mountain torrent to a drainage ditch will suffice; indeed, I have seen them on dry creek beds, waterways only at the Spring freshet.

Dorsalis, in spite of its size, is in character a tolerant, easy-going creature, attending strictly to its own affairs. I have never observed it taking any notice of other species or devouring smaller ones.

On Miller's creek I watched a female for a long while. Having deposited eggs along either shore of the pool by the hovering, perpendicular method peculiar to her kind, she found a place near the centre where a patch of algae was just below the surface. This greatly pleased her, and she remained stationary while she 'spaded-in' 30 or 40 eggs. She then rose to go, and an *Aeschna* male—either *palmata* or *canadensis*—attempted to seize her. The inexcusable and unexpected assault knocked her to the ground, and it required probably nearly a minute to extricate herself from the long grass. When she got on the wing he seized her again. A bush then concealed them from sight, but I hope that she turned upon him (which she was quite large and strong enough to do) and punished him for his importunity.

Walker (1938) records an additional mainland locality: Cultus Lake (Sweltzer creek) August 25th, 1936. In 1940, at Terrace, I am confident that I saw a teneral, but failed to net it. The date, June 18th, would be early for north of 54″.

Flight period: June 10th to August 25th.

Map areas: 1-4. Alaska, type locality, Gloyd 1939.

Petaluridae

Tanypteryx hageni (Selys)

To Dr. W. E. Ricker falls the credit of adding this rare insect to the records of odonate fauna in Canada, and, incidentally, the Province of British Columbia. He took a female on Liumchin creek, July 8th, 1934; and he has, I understand, observed one or two others in the same locality. The creek is distant a stiff walk from Cultus Lake, some 65 miles eastward from Vancouver and near the Washington border. The ancient insect, desiring to continue its earthly existence, could scarcely have chosen a better spot: a statement I make with full knowledge of its inaccessibility and some bitterness—for I have tried to get there!

Strangely enough, due to Dr. Ricker's penchant for rare insects, yet another locality for *T. hageni* has been found by him: this time in the State of Washington: and, more precisely, the White River, Mt. Rainier. He saw some 6 or 7 individuals, and netted 2 males and 1 female, July 21st, 1937. By his great kindness one of the former is in my care. This species was discussed and figured most interestingly by Clarence H. Kennedy (1917, pp. 508-511).

A second Canadian locality by Ricker is Yale (Fraser river—vicinity Hell's Gate) a male, August 30th, 1938. This is a most interesting record, for,

though doubtless a stray from the higher reaches of some nearby creek, it gives promise of further distribution in the Cascade range.

Flight period: July 8th to August 30th.

Map areas: 4.

GOMPHIDAE

OPHIOGOMPHUS COLUBRINUS Selys

This species has been taken from Newfoundland and Fort Severn, Ont., to Hudson's Bay Railway in Northern Manitoba, and again northward in Alberta, so it was a strong 'probability' for this Province. The fact remains, however, that there was no record up to July 15th 1938, when Ricker found it on Cluculz Creek, near Prince George.

Flight period: (based upon the main flight of other species of the genus in the Province) July and August.

Map areas: 10 (northward).

OPHIOGOMPHUS SEVERUS MONTANUS (Selys)

During my residence at Nelson, 1920-1934, I took this species both on the hillside road to the Golf Course, and at Crawford Bay: some twenty-five miles distant on the east side of Kootenay Lake. Like the typical form, *severus*, in Alberta, *montanus* flies from the second week in July to the fourth week in August. Both forms delight in disporting themselves along sunny roads, and to rest upon the warm surface. The females are always scarcer than males: Walker also took it at Nelson.

In view of what Kennedy (1917, p. 534) says relative to altitude, in its possible effect upon the above discussed species, it might be well to state that at Red Deer, Alberta, the habitat of *severus*, the altitude is some 2,700 feet, and at Nelson—Crawford Bay, the localities of *montanus* in British Columbia. 1,700 feet.

Distribution: Buckell (1938) records taking this species: Adams Lake, Aspen Grove, Canim Lake, Chilcotin Lake, Mable Lake, Princeton, Salmon Arm and Summerland, (71 specimens). Some of these localities are in the vicinity of 52″, just north of which I took *O. severus* at Red Deer, Alberta. I am assuming Buckell's specimens all refer to the dark form figured by Kennedy (1917).

Flight period: June 14th to September 5th.

Map areas: 4 (eastward), 5, 6, 7, and 10 (southward).

OPHIOGOMPHUS OCCIDENTIS Hagen

To the four scattered records given by Walker (1927) for this western species, I can add Nelson, West Kootenay district, August 22nd, 1921, a

male. More recently Dr. Ricker reported *occidentis* at Cultus Lake, and during my stay there June 16th-July 20th, 1936, I kept the species under close observation. The first specimen taken was on June 24th, a male; and by July 7th I had netted six more, all males. On July 16th I took two pairs in cop., in fact, in one of these cases—the cluster flying slowly and clumsily —I found that I had a ♀ and two ♂s, so the males must have found females of their species as scarce as I did. However, by July 20th I had secured one more, and had also increased my series of males.

I watched a female seized as she flew over the water: the pair soared high into a tree.

Ovipositing was observed in Sweltzer creek pool in the fish hatchery grounds, at that time teeming with yearling steelhead trout. She flew low over the water, apparently washing eggs from the tip of her abdomen; the operation being concluded by plunging full length onto the water and rising again three times. Two females were noted throughout such performance on July 19th. Why those terminating plunges were taken is obscure, and how they escaped the voracious, watchful trout was nothing short of miraculous. Flying with *occidentis* throughout the period covered above were *Octogomphus specularis, Macromia rickeri,* and *Argia emma,* to mention the more interesting.

On Vancouver Island, 1937, this species was not seen until Forbes Landing was reached July 25th. There it was abundant and continued so until my departure August 22nd. While females were as numerous as males, they appeared to fraternize without thought of sex—in fact I did not see a pair in cop. during my three weeks' stay. The breeding place was the riffles below the hotel, where the Lower Campbell Lake becomes a swift river: there the occasional female was seen ovipositing. The roadways around the hotel were their favorite resting places throughout the day.

Distribution: Walker's (1927) records: Vancouver, Oliver and Peachland, and Sahtlam on Vancouver Island. Buckell contributes: Lillooet and Pritchard. J. Wynne, Enderby, a female, August 14th 1938.

Flight period: June 8th to October 1st.

Map areas: 1-5, and 7.

This is the species figured by Kennedy (1917, p. 541, with mention of *O. phaleratus* Needham, p. 543) as "true *occidentis.*"

Gomphus graslinellus Walsh

Fishing at Christina Lake, Boundary district, the first ten days of July, 1921, I noted one day dragonflies flying over my boat. The spot was the bay of water lilies at the extreme end of the lake, remote from Cascade. One moment I would see a "clubbed" abdomen, and the next green eyes as an insect turned into the sun. A new *Somatochlora* surely! And, wildly excited, I used my landing net "as it shouldn't be used." Disillusionment followed.

They were not one species, but two: *Cordulia shurtleffi* contributing the green eyes, and *Gomphus graslinellus* the club tail, though precise identification of the latter did not come till later. I succeeded in netting three or four specimens: the first record for western Canada.

July 1938 I returned to Christina Lake, and found *graslinellus* on both McRae and Texas creeks. At the former, between the 8th and 12th, I took 7 males and 5 females; the specimens being of recent emergence. With one exception netting was achieved as the insects rested on the gravel roads; but they were extremely wary.

The flight of *graslinellus* when hawking is unique in my experience of western Canadian dragonflies: the insect rising and falling in a switchback course from 3 or 4 feet from the ground to 6 or 7 feet: ~~~~ . I captured one male during such flight, timing the sweep of the net for the low point of the U . Walker informs me in a letter that several related species, such as *Gomphus spicatus, exilis* and *lividus*, practise this strange flight, and points out (which I confirm) that it is an *optional* leisurely gait. Flushed from the road, or frightened by the net, *graslinellus* can fly both straight and fast. Alternating with my captures of the gomphine were those of *Macromia magnifica*, with *Argia emma* occasionally seen.

Buckell supplies one other record for this species: Salmon Arm, 125 miles farther north.

Flight period: June 29th to July 12th. The first date would probably be about correct for emergence, but the insect would unquestionably continue on the wing until the end of August.

Map areas: 5 and 6.

Gomphus olivaceus Selys

Only three individuals of this species have been taken in the Province, and these at three different locations. Walker, a male, at Penticton, July 28th 1926; Wallis, a female, at Peachland, and Buckell, a female, considerably farther north at Pritchard, but still in the dry Transition zone, Oct. 1st. He was fishing in the south Thompson river and it settled on the boat. The landing net was used.

My efforts to secure specimens have been disappointing, though during 1938 I visited Penticton, Peachland and Chase (on the south Thompson) largely with that purpose in view. At the first mentioned only, July 18th-22nd, did I see *olivaceus*. They were very scarce, and those seen pursued a zigzag course in the middle of the Okanagan river—carefully avoiding my boat. A third day I came equipped with a bathing suit and tried standing mid-stream on silt bars. No *olivaceus* would then appear! Once, in the boat, I was within six feet of a fine male. They do not appear to take up any limited reach; but approach, go by, and continue going!

At Chilliwack, July 20th-25th, 1936, I saw a large gomphine settled on a path that was, I think, unquestionably *olivaceus*.

Flight period: July 28th to October 1st.

Map areas: 5.

Octogomphus specularis (Hagen)

This species (specimens had previously been taken by Ricker) was emerging at Cultus Lake at the time of my arrival, June 16th 1936. One teneral was netted June 18th and a number of exuviae were collected at the headwaters of Sweltzer creek, (which empties the lake) where the transformation had taken place on the fish fences and traps pertaining to the hatchery. No new exuviae were noted after June 19th. It should be mentioned that mid-June was wet, and that the emergence, therefore, took place in cool, rainy weather. During the following five weeks 27 ♂s were captured, mostly on the small creek which runs through the hatchery garden. No ♀ were taken, in fact only two were seen.

On August 12th, 1936, *O. specularis* was discovered at the headwaters of Elbow Lake creek, and nine ♀s and two ♂s were netted that day. These were flying with *Cordulegaster dorsalis*, as described by Kennedy, (1917, p. 574) except that the altitude was not more than 1,000 feet, and no great difficulty was experienced in collecting, for, while the country was wild enough, an abandoned logging railroad provided good footing. Nine more ♀s and eleven ♂s were taken August 14th-18th, the latter date yielding but a pair. From emergence to disappearance the flight period in British Columbia can be stated as approximately two months: June 18th-August 18th being actual dates, 1936. *C. dorsalis* was still flying.

Ovipositing was observed, the insect brushing eggs from the tip of her abdomen at intervals of two or more feet, as stated by Kennedy. A pair were seen flying in cop. and these were netted when they settled on a tree over the water.

Where the creek inhabited by *Octogomphus* drains a lake (the case at both Cultus and Elbow Lakes) the insects will venture into the open, the young males to fly a hundred feet and more from their true habitat, and the aged females, at Elbow Lake, to rest on reeds in the sun for lengthy periods. This was the undoing of one female noted, for an *Aeschna eremita* pounced upon her, settled on a bush and ate her.

Since both sexes rest frequently they are easy to net. On the wing, however, the contrary is the case, for not only do the slim, dark bodies present a poor mark for the eye, but at the critical moment they have an annoying propensity of vanishing into the shade.

Flight period: June 10th to August 18th.

Map areas: 4 (southward).

AESCHNIDAE

AESCHNA COERULEA SEPTENTRIONALIS Burmeister

On my Atlin trip (1939) I located a breeding place of this species (previously unrecorded in the Province) on July 8th, and netted 2 males and 2 females on that date; the total series taken to August 28th being 20 males and 10 females. The latitude of Atlin is just south of 60″ north; the extreme northern end of Atlin Lake being in the Yukon. The species occurs, I found, throughout the district where the environment was suitable, but they were never really abundant.

In freshly-taken young males the face is a light grey-blue; and the thoracic markings are clearly defined. The abdomen may be as dark as figured in Walker's monograph, but the majority were lighter. In all my specimens the preocular band is much heavier than as shown by Walker (fig. 3, pl. 22). In both sexes the T-spot is subject to extreme variability: one or both ends of the cross-bar may curve downward to merge into the preocular band; and, in one male specimen, T-spot and band form a solid black spatulate patch. In my total series (both sexes) aberrations as to the T-spot were 25 per cent. Most of my short series of females were too teneral to estimate the ratio of dimorphism in this species. I believe most of them would have developed into the homeochromatic form, but an aged specimen, taken ovipositing on July 14th, was decidedly heterochromatic. The usual overall length of males is 62 to 64 mm., but I have one as small as 55 mm. Females are about 57 mm.

Ovipositing is performed in wet moss patches between tufts of scant grass, or in the creamy-pink muskeg slime bordering small pools, of say 25 to 50 feet in length. They lie flat when so engaged, curving the abdomen to stab in the eggs, and cocking the appendages upward to clear the slime. Walker, in his monograph, comments upon the lack of female appendages in museum specimens; but this I can state is due to the tacky nature of the muskeg slime and not to carelessness on the part of the insects. The net may be placed over them by cautious stalking. If disturbed, they will move on a few feet, or, thoroughly frightened, speed away. The males fly low over the breeding areas searching for mates; and they frequently rest full length on the wet moss or muskeg slime, similarly to ovipositing females.

The habitat is of rather special interest, since the large muskeg pools, with a well-defined solid peaty edge (as favoured by such species as *Somatochlora albicincta* and *hudsonica*) are clearly unsuitable. They require a pool with an edge leveling off into muskeg slime and wet moss, for, as above stated, it is in such the eggs are deposited. These pools are also preferred by *Somatochlora septentrionalis*, and I have seen two males, one of each species, chasing one another in the middle of the pool, and, at the moment, the only occupants thereof. A third species occurring at these pools is *Leucorrhinia hudsonica*.

The flight periods of this species and *A. sitchensis* will doubtless vary north and south of their range; but, judging from my observations at Atlin,

septentrionalis must emerge around June 25th (two or three weeks before it ally) and continue its flight into September: the last specimens taken by me being 2 males August 28th.

Nymph: on July 9th, the day being too cold and cloudy for imagoes, I determined, if possible, to find an exuvia of this unknown nymph; and I searched the species' breeding ground foot by foot. Eventually I got one (a perfect specimen) clinging to a dry grass tuft midst the wet moss, and some ten feet from the water of the pool. In view of Professor E. M. Walker's pre-eminence in this genus, I deemed it only fitting that the description should be his:

Nymph (Figs. 1-4) small and slender, resembling that of *A. sitchensis* but differing in the longer labium and longer lateral spines on the abdominal segments, which are present on segment 6 as well as on 7 to 9.

Head, thorax and wing-sheaths uniform pale brownish, legs of same colour, the femora with the apices and faint traces of an ante-apical annulus, darker. Abdomen light brownish with pale markings as in *sitchensis, interrupta* and *eremita*. An ill-defined median dark band, darkest on segments 8-9, and partially divided antero-mesally on 4-7 by a pale streak which extends caudad from base of segment. The dark median band is bordered laterally by pale bands, laterad of which is a series of subcrescentic spots and a broad marginal pale are just enclosing the lateral muscle scars, which are outlined in brown. Puncta moderately dark.

Head small, postocular margins straight for a short distance then passing in a broad regular curve into the hind margin, which is slightly excavate in the middle. Eyes as in *sitchensis*, moderately prominent, occupying about two-thirds of the lateral margin of the head. Mentum of labium (Fig. 2) reaching a little beyond mesocoxae, like that of *umbrosa* in form, basal breadth about half the apical and less than one-third of the length; greatest breadth three-fifths of length, sides nearly straight and slightly divergent in proximal half, strongly arcuate in distal half; median lobe forming an angle of about 120°, with straight sides; labial palpi broad, the terminal parts parallel-sided, squarely truncate, outer angle not rounded, inner angles without a tooth. Supra-coxal processes (Fig. 3) low and obtuse, the posterior branch much the broader at base, the intervening angle obtuse. Abdomen narrower than thorax, its greatest breadth from segment 5 to 7, lateral spines present on segments 6 to 9, those of 6 minute, those of 7 extending half-way to the base of segment 8, those of 8 three-fourths of the distance to the base of 9, those of 9 to the proximal third of 10. Caudal pyramid two and one-half times as long as the tenth segment. The inferior appendages longer and more gradually incurved at apices than in *sitchensis;* median appendage one-third shorter, lateral appendages two-fifths as long as the inferior pair. Lateral valves of ovipositor just reaching the end of segment 9, the terebra barely longer (Fig. 4).

Length of body 34 mm., mentum of labium 6 mm., hind wing 7.75, hind femur 5.75; inf. apps. 4; ovipositor 2.5; width of head 7; width of abdomen 5.

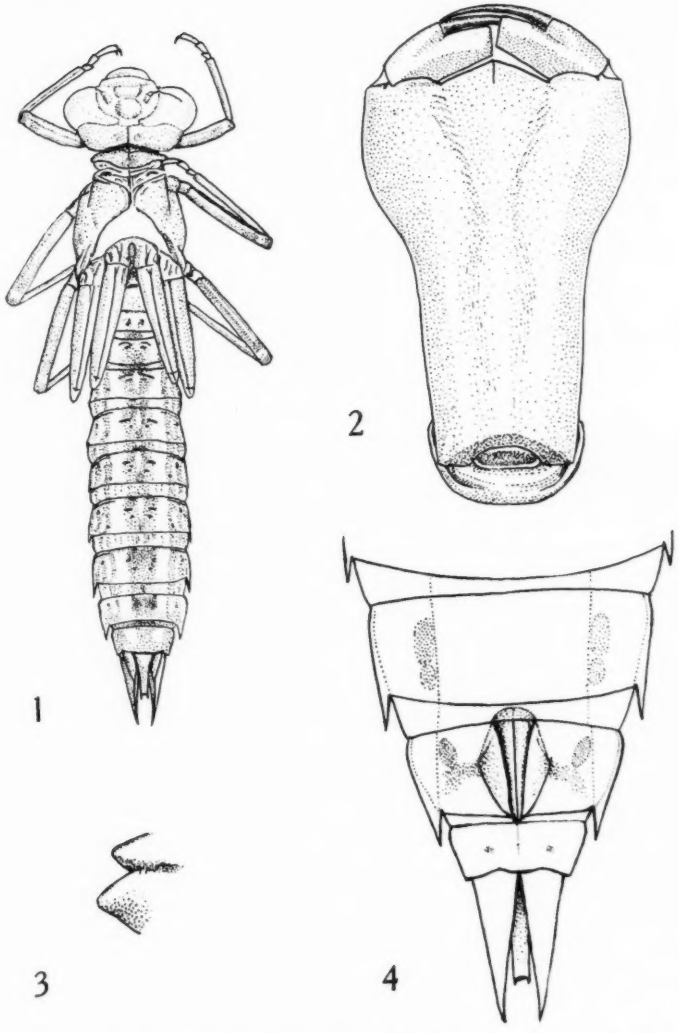


PLATE 1. *Aeschna coerulea septentrionalis* Burm. Fig. 1. Final exuvia, ♀. Fig. 2. Labium. Fig. 3. Left supra-coxal process. Fig. 4 Terminal abdominal segments, ventral view, showing ovipositor.

The nymph of the typical race of this species (*A. c. coerulea* Ström) has already been described by Ris (Mitt. Schweiz. Ent. Ges. XII, 7: 348-354). Comparison of the exuvia of *septentrionalis* with two exuviae (♂ and ♀) of the typical form from the Spiesshorn, Bavaria, confirm the view held by the writer that these two forms are best regarded as races of one species. The Bavarian exuviae are larger with a relatively more robust abdomen, slightly broader labium and somewhat darker coloration, lacking the pale median streak. None of these features, however, appear to be reliable characters, certainly not in the case of the colour-pattern. (E. M. Walker).

Flight period (actual captures) July 8th to August 28th.

Map areas: 13.

Note: Mrs. Gloyd's Synopsis (1939) gives no record in Alaska, but, (p. 15) mention is made to a record from Sitka (Hagen, 1856, p. 381) as possibly this species. The proximity of Atlin to the "panhandle" of Alaska would certainly indicate its presence there at habitats as described in this paper.

Aeschna sitchensis Hagen

When I arrived at Massett, Graham Island, Queen Charlotte Islands, July 17th, 1935, *A. sitchensis*, newly emerged, was the common dragonfly and the only species of that genus then on the wing. For a period of two weeks, both on the roadways at sea level and on the upland muskegs, I had opportunity of observing these insects and their choice of resting places. These were invariably tree trunks, living or fallen, planks in the roadway or the sand in between, and, on the muskeg, twigs of dead bushes: never green vegetation on either tree or bush. My Q.C.I. notes respecting *sitchensis* include the statement that they were "very tame"; and I now recollect that I amused myself upon occasion by plucking them from their resting places with my fingers.

On Vancouver Island, 1937, a short series of this species was taken in the Forbes Landing district between July 26th and August 11th. It occurred in two localities, each the roadway above a cedar swamp. One is situated a mile or so from Lower Campbell Lake on the Upper Campbell Lake road, and the other the pack trail past Upper Campbell Lake camp. To the first mentioned (being readily accessible) some time was devoted, for the possibility of *Somatochlora franklini* or *Coenagrion interrogatum* as flying mates with *sitchensis* was not overlooked. Neither was seen, but individuals of *Cordulegaster dorsalis* would cross the road to follow their creek down into the cedar swamp. There was a strong temptation to do likewise, for I much desired to find *sitchensis'* breeding pot-holes—that must have been there—but consideration of that Devil's Club underbrush always served to check the impulse.

Distribution mainland, south of 52″, Prince Rupert (E. M. W.) Field (E.M.W., E.R.B., F.C.W.) August 10th, Jesmond (E.R.B., F.C.W.) August 29th.

On my visit to Atlin, B.C., 1939 (60″ north) nothing was seen of *A. sitchensis* until July 14th, when a female was taken emerging with her exuvia.

At the same habitat on that day *Somatochlora franklini* was flying, and an aged *Aeschna coerulea septentrionalis* was netted ovipositing. My further captures of *sitchensis* were as follows: July 18th, a young male; August 8th, a homoeochromatic female; August 9th, 2 males; August 21st, 1 of each sex.

The above paragraph suggests three points worthy of comment: (1) a further confirmation of *A. sitchensis* as a flying companion at the habitat of *Somatochlora franklini;* (2) the relative dates of emergence of *sitchensis* and its ally, *A. c. septentrionalis* at the same habitat: the latter appearing, as I estimate it, two or three weeks earlier; and (3) the comparative rarity of *sitchensis* to its ally at that latitude. This, I take it, would be the true range of *A. c. septentrionalis,* but well northward in the range of *sitchensis.* Walker (1927) records finding one or two *septentrionalis* at Banff, Alta., June 29th 1913, "in company with *A. sitchensis,* which was common." There (51″ north) *sitchensis* would be the species in its true territory, and *septentrionalis* at the extreme south of its range. Relative to these views, Walker warns me that we have no positive knowledge that *sitchensis* does not range as far north as its ally. I, therefore, qualify the argument as my personal opinion in the matter.

My trip of 1940 provided a record for *sitchensis* in the area, Rocky Mountain Range, north, viz, at Mount Robson, August 4th. This, of course, was to be expected, but the territory had, previously, not been worked. It was flying with *Aeschna juncea, eremita, palmata, umbrosa* and *interrupta lineata,* with *Somatochlora semicircularis* in abundance.

Flight period: (Actual captures) July 14th to August 29th. It would undoubtedly emerge earlier, and fly later, than these dates would indicate.

Map areas: 2, 4 (northward) 8, 9, 12 and 13. Also Alaska, Gloyd 1939).

Aeschna juncea L. (race americana Bartenef)

To the three widely separated records for British Columbia given by Walker (1927), viz., Inverness, Prince Rupert, and Grouse Mountain, Vancouver, I can add Port Clement, Queen Charlotte Islands, two ♀s, July 31, 1935; and the same year, on Vancouver Island, Forbes Landing, August 9th, a ♀, and Courtenay, August 13th a ♂.

My 1937 trip on Vancouver Island produced but two records for this species: southward, at the junction of Waugh and Goldstream creeks, July 4th, 2 females; and on the "Forbidden Plateau," Courtenay (3,200 ft.) August 26th, 5 males. The first of these was quite unexpected, being a low elevation for *juncea,* so far south. The second is a typical habitat, and the Courtenay record of 1935 was doubtless a stray from the Plateau.

Distribution mainland: I have records Field, August 8th-11th 1938, common; Kamloops (Lac le Jeune) August 24th, a male. Buckell adds: Leanchoil, Lumby, Penticton, Quesnel and Sinclair; and Ricker contributes, Cultus Lake (Liumchin Mt.) August 26th.

On my visit to Atlin, 1939, (60″ north) young males, just come to adult coloration, where first taken July 15th, and the flight continued until the end of August, when I left for the south.

Females, of both colour forms, were observed ovipositing around the edge of muskeg pools on many occasions: reed stems being grasped and the abdomen being lowered some two inches below the surface to the muskeg slime.

On my trip of 1940, I took this species in the Yellowhead Pass, at Mount Robson, August 4th, 2 males.

Flight period: June 16th to August 28th.

Map areas: 1-6, 8-13. Mrs. Gloyd's Synopsis (1939) provides a number of records in Alaska.

Aeschna subarctica E. M. Walker

At the time of publication of his monograph (1912) Walker believed this species confined to the Canadian zone—Atlantic Coast to Manitoba; and to the date of his "The Odonata of the Canadian Cordillera" (1927), there was still no record to upset such belief. Then, August 26th 1934, Buckell took *subarctica* at Field, a single male.

To establish the species further as a native of British Columbia, a male fell to my net on Vancouver Island, Courtenay (Northey's Lake and Black creek) August 13th, 1935. But if Walker overlooked British Columbia as a possible region for *subarctica*, it was not for lack of knowledge of the species. I quote his monograph, page 100: "*Ae. subarctica* is closely related to *Ae. juncea*. . . . these two species fly together at Nipigon, Ont." To which I may add, so they do at Courtenay—see my record for *juncea* there, of the same date. The natural law implied here, *the association of species under like environment*, while often at fault can, upon occasion, give the field worker a great thrill.

On my trip of 1940, I located *subarctica* at Tête Jaune, (the entrance to the Yellowhead Pass) August 12th, netting 4 males: the habitat being the muskeg pools bordering a large reedy slough. The day was unfavourable, being both cloudy and windy. Two days previously I had netted several aeschnas on the slough proper: *palmata*, *eremita* and *umbrosa*, but not *subarctica*. Now, on the muskeg pools, my four captures were all that species. Probably to avoid the wind, the insects were flying low, just over the tips of the moss rising to the surface of the water. My specimens were all netted at one pool, at the only spot it could be approached. Assuming that the species was also flying at the other unapproachable pools, then it is obvious that the insect is not rare at this habitat: Lat. 53 N., altitude, 2,600 ft. I did not take *Aeschna juncea* (*subarctica's* usual flying mate) at Tête Jaune, but I had taken both *Aeschna juncea* and *sitchensis* at Mount Robson, 18 miles to the east, and they doubtless occur at Tête Jaune.

Flight period: (actual dates of capture) August 12th, 13th and 26th. A safe assumption would be early July into September.

Map areas: 2, 8 and 9.

AESCHNA INTERRUPTA Walker

The four *races* of this species, as described by Walker, present an interesting but somewhat difficult example of geographical forms, and the intermediate varieties resultant where the respective territories of two of these forms converge. In this paper it would be out of place to discuss the *Ae. interrupta* problem at length, but since in British Columbia it reaches the acute stage, a brief outline as to the distribution of the *races* appears necessary.

(a) AESCHNA INTERRUPTA INTERRUPTA Walker—This is the eastern race, occurring—north of the international boundary—from Newfoundland to Ontario.

(b) AESCHNA INTERRUPTA LINEATA Walker—The Prairie-country *race*, occurring from the Rocky mountains in Alberta, through Saskatchewan and Manitoba to western Ontario.

My trip 1940, I took specimens of race *lineata* (passed upon by Walker) in the Yellowhead Pass, at McBride, Tête Jaune and Mt. Robson, July 15th-August 11th.

Map areas: 9.

Note: As must be expected, between the two great areas of distribution for the above mentioned races of *interrupta*, a "no-mans-land" occurs, which Walker has found to be the Patricia section of the Kenora District in western Ontario. Here variable forms will be taken leaning towards one or other of the *races* to east and west.

(c) AESCHNA INTERRUPTA INTERNA Walker—This race is the most southern of the group, occurring in the high mountains of New Mexico and continuing northward through the eastern American cordillera to appear in British Columbia in the territory between the Rocky and Gold ranges, that is, centering upon the Selkirks.

Structural characters of the superior appendages serve to keep this race distinct: "A slight ventral prominence at the base, seen best when viewed obliquely from above. The lateral thoracic bands are typically wider in *interna* than in *lineata*." (Walker, in a letter.)

At Nelson, in the Kootenay District, Walker and myself took specimens of *interna;* and at Golden, August 14th 1938, I netted a good series which were referred by Walker to this race: "about as pronounced as it ever is in British Columbia." I have also specimens from Field.

Map areas: race *interna*, 6, 7 and 8.

(d) AESCHNA INTERRUPTA NEVADENSIS Walker—This race, also belonging to mountainous country, has been taken (Kennedy 1917) at high altitudes

in California. Its range is westward of *interna* territory in both the American and Canadian cordillera, occurring in British Columbia between the Gold and Cascade ranges, and westward to the coast. Many of the records throughout the Okanagan District and northward to Kamloops, etc., are referable to *nevadensis*.

Note: Sandwiched in, as in *interna* between the territories of *lineata* and *nevadensis*, off-type specimens abound throughout the entire interior area; and it is for this reason that I am not attempting to define the range of each race except in a general manner.

Map areas: race *nevadensis*, 5 and 4, blending into the coastal form in areas 3, 1 and 2.

Coastal area: On reaching the coast, including Vancouver Island, *nevadensis* grades into a form resembling the eastern race *interrupta* in that the thoracic markings are frequently reduced to spots, but differing from that race in various slight details such as those of proportion of parts. This form probably deserves a racial name but as it has not yet been critically studied, it must remain provisionally in the race *nevadensis*. Walker records this form from Prince Rupert and the Nanaimo district, Vancouver Island. I have taken it from Vancouver (mainland) to Forbes Landing. Vanc. Is.

Map areas: 1, 2, 3 and 11.

Flight period: (all races) 3rd week July to mid-September. Extreme dates: June 25th to October 8th.

Note: Mrs. Gloyd (1939) gives records of races *interrupta* and *lineata* in Alaska. The former is possibly the form discussed above under "Coastal area."

Aeschna eremita Scudder

In the Massett district, Queen Charlotte Islands, the second half of July 1935, this species was associated with *Aeschna sitchensis:* first emergence of both having occurred prior to July 15th. I took several specimens of *eremita*, both sexes, July 19th-30, but it was less common than the typical muskeg species in a terrain largely of that character. My Vancouver Island records are: Forbes Landing (Mud Lake) August 9th-11th; Courtenay (Northey's Lake) August 13th-14th. In 1937, on the Island, this species was flying at Forbes Landing, July 25th to August 18th, when I left.

On the mainland, Harrison Bay (Elbow Lake) August 14th 1936; Field (Ottertail creek) August 10th; Kamloops (Lac le Jeune) August 24th 1938, very common. Buckell records 18 additional localities from the southern interior of the Province north to Prince George. Walker (1927) records the taking of *eremita* at Vancouver and Peachland; and Wellington, Vancouver Island, and gives Atlin (E. M. Anderson) and Daisy Lake, Garibaldi district (G. A. Hardy).

On my Atlin trip, 1939 (60″ north) this species was already upon the wing July 6th, but the insects were young and their exuviae were in evidence, indicating recent emergence. By July 15th *A. juncea americana* had appeared as a flying companion at the larger muskeg pools. In spite of adverse weather conditions, including frost on the nights of August 3rd and 11th, the flight of *eremita* continued until August 31st, when I left for the south.

In 1940 I took this species northwards, in the previously unworked territory: McBride, July 15th; and, more eastward, Tête Jaune, August 8th and Mount Robson, August 4th.

Flight period: June 19th to September 2nd.

May areas: 1-10, 12, 13. Alaska, see Gloyd (1939).

Aeschna canadensis E. M. Walker

Walker (1927) gives but three localities for this species: two southerly on Vancouver Island, and at Vancouver. I found it common on the Island at Forbes Landing (Mud Lake) August 9th-11th, 1935, and again in 1937, July 25th to August 18th, when I headed south.

On the mainland, my records, besides Beaver Lake, Vancouver, where it flies until the end of September, are: Chilliwack, July 22nd-24th; Hope (Kawakawa Lake) July 28th, Harrison Bay (Echo Lake) August 9th. Buckell records: Malakwa, Salmon Arm and Prince George (Summit Lake).

Hunting for flies, it will follow the contour of the lake shore, entering and searching the low bushes in a most systematic manner. It is consequently very easy to net. At Forbes Landing, it was one of the *Aeschnas* flying on the Lower Campbell Lake shore at dusk. In point of fact *canadensis* in that district was a nuisance, for with nine species of the genus on the wing, I was searching for two more. This meant that every passing *Aeschna* must be netted for positive identification.

Flight period: July 25th to September 29th.

Map areas: 1-6, 10.

Aeschna tuberculifera E. M. Walker

This was another species believed to be eastern in its habitat, until Walker himself took it in the Nanaimo district and, in larger numbers than he had ever taken it in the east. Considerably farther north on Vancouver Island, Forbes Landing, I netted a fine male, August 9th 1935, and the probability is that others were there. But with the swarms of dragonflies on the wing—including six species of the genus *Aeschna* and three of *Somatochlora*—one net had its limitations in a short visit.

In 1937, the three weeks spent at Forbes Landing served to prove that of the nine species of the genus there flying *tuberculifera* had good representation. It was possibly most abundant over the roads and grass plots around

the hotel, but specimens were netted at Miller's creek and Upper Campbell Lake, respectively ten and sixteen miles distant. An ample series was obtained. I found that care was necessary in netting females, the appendages being delicate and prone to break off.

The females taken were homoeochromatic without exception; indeed, the likeness to the male was not only in the blue coloration, but in the long graceful body.

Ovipositing was observed on several occasions at Mud Lake, near Forbes Landing. The insects—sometimes side by side—would alight on the slim stemmed sedges rising from shallow water. With a hold, possibly four inches from the surface, they would curve their abdomens and punch eggs into the sheafed stem. This was mid-August.

Flight period: (Actual dates) July 26th to August 19th. It is safe to assume that the full flight would be from early July well into September.

Map areas: 1 and 2.

Aeschna palmata Hagen

I have records for this species from July 7th to November 1st; but, in the same district, it does not precede *Aeschna umbrosa* by more than a few days.

Walker (1927) gave scattered records for *palmata* over a wide territory, commencing with Atlin in the north, and I will select localities from my list best serving to present new ground. Queen Charlotte Islands, Massett tide flats, two ♀s netted and others, both sexes, seen July 27th-30th 1935. Vancouver Island, northerly, Forbes Landing, August 10th; Courtenay (Northey's Lake and Black creek) August 13th; and, 1937, "Forbidden Plateau," (3,200 feet) flying with *Aeschna juncea americana*, August 26th.

Mainland: Vancouver, August-November 1st, and Grouse Mountain, 4,000 feet, August 20th; Lulu Island, August 21st; Cultus Lake, July 7th; Chilliwack, July 24th; Hope district, (Silver creek and lake) July 25th-27th, (Kawakawa Lake) July 31st, (Little Mountain) August 1st, (Hope-Princeton trail) August 2nd, (Texas Lake) August 3rd; Harrison Bay, August 9th, Penticton, Vernon, Revelstoke, Field, Golden, Kamloops, Clinton, July 15th-August 28th. Buckell gives 42 localities, and Ricker 6.

The males of this species vary, even in the same district, in that some have the triangular medio-dorsal spots blue, and some yellow. In insects of apparently the same age, and probably bred in the same water, the factor affecting the pigmentation of these spots is an interesting question.

On my Atlin trip, 1939, (60″ north) I found *palmata* less common than I had expected, those netted being: 2 teneral males July 17th, a pair in cop. July 20th and a single male August 22nd. Its usual flying companion farther south, *A. umbrosa*, was not in evidence, though Walker (1927) records latitude 62″ north within the range of this species.

In 1940, I took *A. palmata* at two habitats in the Yellowhead Pass: Tête Jaune, August 8th and Mount Robson, August 1st to 7th.

Flight period: July 1st to November 1st.

Map areas: 1-13. For Alaskan records see Gloyd (1939).

AESCHNA UMBROSA, and race OCCIDENTALIS E. M. Walker

This is the last of the genus to emerge, my earliest date being Cultus Lake, July 20th 1936. It is usually associated with *Aeschna palmata*, and both species last out the season to the end of October, or prior freeze up: indeed, I have taken it subsequent to several degrees of frost. At Hope and Harrison Bay *umbrosa* and *palmata*, very numerous, flew until dark, and I caught and released dozens to arrive at which had the advantage in numbers. It worked out about a tie.

Umbrosa varies from ultra-dark specimens, with the P.D. spots in the male much reduced and green in tint, to individuals having such spots considerably larger and blue in tint: that is, the race *occidentalis*. Intermediates between these extremes may also be taken. At Beaver Lake, Vancouver (easily accessible to me) I take all shades.

My records, Vancouver Island: Campbell River, August 8th; Forbes Landing, young specimens, July 26th. By August 18th, when I left, they were fairly common, but some were still teneral.

Mainland: Vancouver, August-October, inclusive; Cultus Lake, July 20th; Hope (Silver creek and Kawakawa Lake creek) July 26th-31st; Harrison Bay (Echo Lake creek) August 9th, Golden, August 14th; Jesmond, August 29th. The last two records were race *occidentalis*.

I give a selection of localities by both Walker and Buckell.

Race UMBROSA: Walker (1927) Yukon Territory, Departure Bay, Vancouver Island; Nelson, Kootenay Lake; (1938) Cultus Lake, Sumas Game Preserve, Fraser River. Buckell (1938) Smithers, Quesnel.

Race OCCIDENTALIS: Walker (1927) Prospect Lake, Shawnigan Lake, Wellington, Grenwood. Buckell (1938) Creston, Falkland, Golden, Mabel Lake, Okanagan Landing, Quesnel, Vernon and Wasa.

Apart from these two races (the status of which remains undetermined) I took at Forbes Landing, Vancouver Island, several specimens of a third interesting form. This is ultra-dark, small in size, and having an extremely thin abdomen. Walker (1927) mentions taking a specimen at Departure Bay, Vancouver Island, "an abdomen almost black with no traces of the postero-dorsal spots." These records are given here for the benefit of future collectors on Vancouver Island.

In 1940 I took typical *umbrosa* in the Yellowhead Pass at Tête Jaune,

August 8th, and, more eastwardly, Mount Robson, August 4th, and Red Pass Jct., July 25th.

Flight period: July 19th to October 30th.

Map areas: 1-10. The fact that *umbrosa* is usually late in emerging quite probably explains the absence of records from areas 11, 12 and 13, and also Alaska, for Walker (1927) gives records from Yukon Territory: Lat. 62″-63″.

Aeschna constricta Say

Up to the date of Walker's paper (1927) the only record for *constricta* was a single female taken by himself, August 16th, 1913, at Okanagan Landing. Buckell, however, proved it to be well established in the Province when he took a series of 20 at Creston, August 22nd, 1934; and this was additionally confirmed in 1939, when J. Wynne took specimens at Enderby, August 6th.

Flight period: collected specimens are for the month of August, but based upon the flight periods of its allies, *(palmata* and *umbrosa)* the warm southern territory where it occurs, and its season in Ontario, it is safe to assume an emergence about the third week in July and a continued flight certainly into October.

Map areas: 5 and 7.

Aeschna californica Calvert

Unlike most of the species of the genus in British Columbia, the flight period of *californica* becomes definitely over before August. In size no larger than *Aeschna sitchensis,* it emerges with the earliest spring dragonflies: *Enallagma boreale, Libellula quadrimaculata,* I found a male transforming at Beaver Lake, May 7th 1935, in the sunshine of the forenoon, but I have no other evidence of daytime emergence for this species as an exception to the general custom of the genus. When mating the pair fly around seeking a place to alight, when they rest for some time.

My records serving to add new territory to the locations given by Walker (1927) are: mainland, Vancouver, May 7th to the end of July; Cultus Lake, June 18th-24th; Chilliwack, July 25th.

My 1937 records on Vancouver Island were: Sooke, June 7th; Thetis Lake, June 14th; Florence Lake, June 29th-July 4th. Nanaimo district: Wellington Lakes, July 14th and Newcastle Island, July 16th. Forbes Landing, a male flying with *Aeschna eremita, multicolor* and *canadensis,* July 25th. This was the last seen and the date, it will be noted, tallies exactly with my final record on the mainland of the previous year!

Further records: Kaslo, June 19th, and Crawford Bay, June 28th 1938 (F.C.W.); Sumas canal and Liumchin creek (Ricker) May 5th-June 23rd;

Aspen Grove, Adams Lake, Salmon Arm, Squilax, Tatla Lake, Osoyoos, Vernon, Westbank, (Buckell) May 16th-July 4th.

Flight period: April 24th to July 25th.

May areas: 1-5, 7 and 10 (southward).

AESCHNA MULTICOLOR Hagen

This species may be readily identified on the wing, even at some distance, by its light blue face. At Vancouver it is the second *Aeschna* to appear, being usually three or four weeks later than *californica*.

Walker (1927) gives two mainland records for the species, Vancouver; and Ainsworth, West Kootenay district. My south Fraser Valley captures serve to fill this gap partially: Cultus Lake, June 25th; Chilliwack, July 17th; Hatzic Lake, August 8th; Cloverdale, (Nicomkle River) September 5th.

Walker's records for this species (1927) do not extend north of the Nanaimo district on Vancouver Island. I took it all along the route of my trip, 1937, viz: Thetis Lake, June 22nd; Florence Lake, very common, June 29th-July 4th; Nanaimo district: Departure Bay, July 8th; Wellington Lakes, July 14th; and Newcastle Island, July 16th. Courtenay (Northey's Lake and Black creek) July 20th. Forbes Landing, less common than some of the species of the genus, but sharing honours with *Aeschna palmata* at Mirror Lake, July 25th-August 18th.

Distribution: further records: Crawford Bay (Kootenay Lake) (F.C.W.) June 28th and Christina Lake, July 3rd-14th, 1938; and Buckell contributes: Adams Lake, Salmon Arm and Squilax. Enderby, June 18th 1939, J. Wynne.

On my trip of 1940, Prince Rupert to the Alberta border, I found this species flying at McBride, July 12th to 19th, at a large horseshoe-shaped slough, believed to have been a former channel of the Fraser River. Walker (1927) places *multicolor* in the Western Austral or Sonoran Fauna, and since McBride is north of Lat. 53″, the insect would appear to be well out of its range as understood at that time. However, it was quite common, flying with *Aeschna eremita* and *interrupta lineata* and nine other species of Odonata, all typical of the Canadian Zone.

Flight period: May 18th to October 3rd. The height of its season is mid-June to mid-August.

Map areas: 1-7, and 9, at McBride.

ANAX JUNIUS (Drury)

This species is far from common in western Canada, in fact I collected dragonflies in Alberta and British Columbia for twenty years before seeing one. When I was at Chilliwack golf course sloughs, 1936, an adult was on the wing July 15th-17th, but it would not come within netting distance, and another was seen August 8th at Hatzic Lake. Then, at Squawcum Lake,

Harrison Bay, August 15th-19th, a true habitat for *junius* was discovered: and the first actual breeding record for the Province. These were recently emerged males and females, (the latter predominating) and as yet uninterested in sex: at least none were observed in cop. As many as ten were seen in the air at one time; and ten ♀s and four ♂s were netted.

My 1937 trip on Vancouver Island, over the length of the highway, provided records as follows: Thetis Lake, June 24th and 27th; Florence Lake, June 30th, and at a nearby small lake, an aged female ovipositing, July 5th. Wellington Lakes, July 12th; Forbes Landing an individual seen July 25th, and a male netted, flying with the aeschnas on the lake shore, August 15th. My experience at Squawcum Lake, 1936, set the time of emergence to mid-August (also the time in Ontario) and I questioned whether any of the records given above were local bred insects, except the last at Forbes Landing —which was probably a stray from one of the lakes farther south.

Distribution: Buckell records Salmon Arm and, southwardly, Oliver and Osoyoos. The last mentioned was July 2nd 1937 (subsequent to his published list) and he gives me a notation "ovipositing in tandem among water weeds." He netted 2 males and 1 female. Osoyoos is close to the Washington boundary and these insects may have come from much farther south.

Flight period: May 18th to September 6th, with the probability of those recorded earlier than August being migrants from the south. The insects of British Columbia, of August emergence, would, of course, fly much later than the last date given, September 6th.

Map areas: 1-5. For Alaska see Gloyd (1939).

Corduliidae

Macromia magnifica McLachlan

There are two positively established habitats of *magnifica* in British Columbia: the Okanagan river, between Penticton and Dog Lake; and Christina Lake, in the vicinity of McRae creek. At the former locality Walker observed the species July 22nd and 23rd 1926, and I netted 10 males there July 18th to 22nd 1938. At the latter I took 6 males and 5 females July 3rd to 12th 1938.

Walker (1927) records 2 males by Wallis at Peachland, July 24th and 31st 1909. These may have been locally bred insects from either Trepanier or Deep creek, or again, they might have been strays from the Okanagan river to the south. During my visit to Peachland July 22nd and 23rd 1938 I saw no *Macromia*. Buckell also publishes a record: Vernon. This single specimen was taken by Bird at Deep Lake, which failed to impress me as a breeding place for *magnifica*. It was in all probability a stray from a river or creek in that district.

At Christina Lake my captures were all on roads, and, in spite of the insect's powerful flight, a comparatively simple matter. The technique is the

same as with *M. rickeri:* watch it coming, wait until it is alongside, and swing with the net as it goes past. Its boldness is its downfall. On the Okanagan river I used a boat and rowed centre stream. Observing a *magnifica* hawking along the bank, I would give two hasty strokes and clutch a bush to steady my craft against the stream. On his return trip he would probably be within netting distance, or, if not, on the following one, for his reach is of no great length. If bushes or other obstacles prevented the boat from reaching the bank, I would get as close as possible to crowd the insect inshore. I found that these males were generally in pairs, and that one safely netted, it paid to remain stationary for the companion to come along.

At Christina Lake, associated species were *Argia emma* and *Gomphus graslinellus,* and on the Okanagan river, *Argia emma* and *Gomphus olivaceus.*

Ovipositing was observed at the latter habitat, but this has been described by Kennedy (1915), and is the same as stated by me for *Macromia rickeri.*

Flight period: (specimens collected) July 3rd to July 31st, but the true flight would be undoubtedly as long as that of *rickeri,* mid-June to the second week of September.

Map areas: 5 and 6.

Macromia rickeri E. M. Walker

This new species, discovered by Dr. Ricker at Cultus Lake, and described by Walker (1937), yielded a good series during my stay at the lake June 16th-July 20th 1936: viz., 21 ♂s and 3 ♀s.

By July 28th I had moved to Hope district, and on this date at Kawakawa Lake an aged ♂ was netted. Keenly interested to learn whether this might be a stray from Cultus Lake, forty to fifty miles distant, or an additional habitat, I worked the lake assiduously. On August 4th two ♂s were seen flying together; August 5th netted a mature ♂ and ♀; August 6th I watched a ♀ ovipositing. The question was answered.

At Cultus Lake the mature nymphs live under stones, and, when I was staying there, eleven were collected and 'pailed' June 17-23rd. Of this total five emerged safely, four being ♀s. These were kept alive two to three days to mature as far as possible, but unfortunately all in the end had to be thrown away, having been spoiled by parasites. However, besides their exuviae, the captive nymphs yielded points of interest. The first emerged about 8 a. m. June 23rd, and by 11 a. m. had spread her wings. The other four (and three more that died in the process) climbed up the sticks provided in the early evening, remaining with head and shoulders out of the water until dark. Transformation took place between 10 and 11 p. m. Assuming that the captives behaved as under natural conditions, it would appear that (1) the insect accustoms itself to atmospheric conditions for about five hours before daring the great adventure, and (2) that, like the aeschnas, it is ready for flight and safety before dawn.

June 25th a pair were taken in cop., my earliest date of sexual maturity.

At Kawakawa Lake, where the shore line is not stony, the ovipositing ♀ flew quickly some eight or ten inches above the water, swooping down every five or six feet to touch the tip of her abdomen. The water was five to ten feet deep, with a muddy bottom and reeds well below the surface.

While a very fine flyer, *rickeri* is not particularly difficult to capture on the wing, for, like the aeschnas they will take a fairly definite reach for a few minutes; and they are bold enough to fly within netting distance. True, I used a British "kite" net, 24 by 17 inches, the efficacy of which they may have underestimated. Occasionally specimens may be taken at rest.

Distribution: Besides the two localities given above as occurring in the southwest corner of the Province, Buckell records 2 specimens at Salmon Arm, approximately 125 miles due northeast, and not very far north of a *M. magnifica* record.

Flight period: June 16th to September 10th—the latter date by kindness of Ricker.

Map areas: 4 and 5.

Note: The destruction of my specimens was wrought by the grubs of a minute fly, of which I found the white larvae, brown pupae, and black imagoes all present in the box of papered Odonata two or three weeks later; when the *M. rickeri* had to be discarded, other specimens salvaged, and the box thoroughly cleaned. My view was that the eggs were deposited in the *rickeri* during their captivity under an insect net, out of doors in the sun. I regret that I no longer remember whether the flies were two-winged or four, though I satisfied myself at the time. This is the only occasion in my experience of parasite trouble with newly killed specimens, i.e. where the live dragonflies must have been attacked.

Tetragoneuria spinigera Selys

The mainland record of Cultus Lake can now be added to the several Vancouver Island localities given by Walker (1927). Six ♂s were obtained by me in the vicinity of the lake, June 21st-30th, and one damaged ♀ was taken from the radiator of a car.

I had not previously taken insects of this genus; and I was impressed by the unusual colour of the eyes: a peacock blue, comparable in its translucent depth to the green eyes of the *Somatochlora* group. This colour in freshly caught specimens has doubtless been commented upon by other authors, but I have failed to note it. With drying the eyes become a dull brown.

On Vancouver Island, 1937, I took this species from Sooke, in the extreme south, June 12th, to a northern record at Forbes Landing. At the latter camp my last capture was a female, July 30th. She had been resting on a cedar bough overhead, and, attacked by a robber fly, dropped, still in its grasp, to

the table. Early in the insect's flight period I fousd females difficult to obtain, but later, at Thetis Lakes and Florence Lakes they might be seen flying along the shore and, in some cases, with an inch of the egg-ribbon hanging. The lateral view of females in flight gives the illusion of miniature sea-planes, due, apparently, to the tip of the abdomen being canted upward and a glimpse obtained of the forked vulvar lamina; but, once netted, the peculiarity is gone.

Needham (1901) wrote of *Tetragoneuria* egg masses to be found in lakes, and, to give a conception of bulk, mentioned a barrel. At Florence Lake, June 28th to July 7th, I examined clusters of egg-ribbons (one on either side) too large to be contained in cupped hands, and to which scores of females must have contributed once the initial 'nest eggs' were placed. At the top of the mass would be several braids of recent placement: these of a blue-grey coloration. Beneath these the mass, bleached by the sun and dirtied by the water, would gradually grade to an uninteresting brown. The eggs in newly placed braid are yellow in colour, the shape oblong.

At Thetis Lake this species was emerging in numbers June 16th, the nymphs crawling over the grassy slope and gravel pathway and transforming on the seats and fencing. The distance traversed was 20 feet.

Distribution mainland: Cultus Lake (Ricker and F.C.W.) Kaslo, June 6th-19th; Crawford Bay (Kootenay Lake) June 28th; Christina Lake, July 1st-9th 1938, and egg masses (all F.C.W.). Buckell contributes Squilax and Vernon. Walker's (1927) records, confined to Vancouver Island, were Alberni (Carter) Nanaimo district (Huntsman), Victoria, Langford Lake and Goldstream (Osburn).

Flight period: June 6th to July 30th. At Kaslo, June 6th, they were fairly common and the emergence must have been some days previous.

Map areas: 1, 2, 4, 5, 6, and 7.

Tetragoneuria canis McLachlan

It seems strange that in a Province where *Tetragoneuria spinigera* can accommodate itself over so wide an area, the range of *canis* is confined to the Sumas canal sloughs. Here Ricker discovered it May 11th 1933, and he has subsequently found it abundant there in May and June.

On June 9th, 1940, I visited the Sumas area and I found the species flying at sloughs along the highway for several miles. The 2 males netted were young, and no females were in evidence.

On my trip of 1940, Prince Rupert to the Alberta border, a northern station was discovered for this species at Burns Lake, just north of Lat. 54″. The first specimen netted was at a slough on June 29th, but I later found that the insects were fairly numerous on Burns Lake itself, flying over the water lilies along the shore, July 5th.

Needham, writing of *Tetragoneuria spinigera* (1929), states: "it is the most northern of the genus," but the above Burns Lake record for *canis* is more northerly than any for *spinigera* in British Columbia to date: indeed, by a margin of 200 miles.

Flight period: May 11th to July 5th; but at the latter date, at Burns Lake, they were still plentiful.

Map areas: southerly in 4, and, north of Lat. 54″, in 10.

CORDULIA SHURTLEFFI Scudd.

This is an early summer species, emerging with *Enallagma boreale, Aeschna californica, Libellula quadrimaculata,* etc. I have records at Beaver Lake, Vancouver, from May 2nd to August 21st; but the fourth week in May to the fourth week in June is the peak of the flight.

Walker (1927) gives a long list of records, covering wide territory, and I contribute the following additional localities: Queen Charlotte Islands, Massett, July 20th 1935, a ♂; Vancouver Island, northerly, Forbes Landing, August 9th-11th 1935; mainland, Boundary district, Christina Lake, 1st week July 1921; Lower Fraser Valley, Hope, August 2nd 1936, a ♀.

On my 1937 trip up Vancouver Island I found this species consistently present, south to north: Sooke (Young's Lake and pool on highway) June 12th; Thetis Lake, June 21st; Florence Lake, June 29-July 4th; Nanaimo district. Wellington Lakes, July 14th, and Newcastle Island, July 16th; Courtenay (Northey's Lake and Black creek) July 20th; Forbes Landing district: Lower to Upper Campbell lake, July 25th to August 18th: by the latter date the flight appeared to be about over. The "green-eyed" *shurtleffi* can be somewhat of a pest in districts where the collector is intent upon the similarly "green-eyed" *Somatochloras.*

Distribution: localities selected from lists to indicate extent of range: Walker (1927) Atlin, Prince Rupert, Cranbrook district, Revelstoke, Nelson & Kaslo. Ricker (1938) Sumas Canal slough. Buckell (1938) Barkerville, Prince George, Kamloops, Salmon Arm, Princeton etc.

On my trip of 1940, Prince Rupert to the Alberta border, I took this species at Terrace, June 17th; Smithers, June 22nd, Burns Lake, July 5th and McBride, July 15th.

Flight period: May 2nd to August 21st.

Map areas: 1-7, 9-13. For Alaskan records see Gloyd (1939).

SOMATOCHLORA WALSHII (Scudd.)

This species—of which I took a female at Nordegg, western Alberta, July 15th 1917—had escaped the attention of collectors in British Columbia until August 9th 1935, when I netted a male at Forbes Landing, Vancouver

Island. The precise locality was Mud Lake. Then on the mainland, at Harrison Bay, on the abandoned logging railway to Echo and Elbow Lakes, another lone male fell to my lot: the date being August 10th 1936.

In 1937 I devoted three weeks of my Vancouver Island trip to Forbes Landing district, viz., the last week in July and the second and third in August. Throughout this period *walshii* was on the wing, and might be taken on four separate creeks. The most prolific of these was the drainage waterway between Mirror and Echo Lakes, some two miles on the road to Upper Campbell Lake. In all, I took over 40 males and 9 females, without making any serious inroad into the available supply.

Males, when not visiting the water, would fly together in nearby sunny glades at the edge of the conifers. A number of females were observed in process of ovipositing and were watched most carefully at the stagnant pot-holes of the drainage creek above referred to. The insect would fly down to the surface of the water amid the broad-leaved reeds, going from one small open space to the next, the dip, dip, dip, of her abdomen never ceasing except when she manoeuvred around the reed stems. Some scores of eggs must have been released at one laying and within an area of three or four feet. Intent upon her task, she would be oblivious of the net held in readiness two feet above her. The eggs disposed of, she would rise to just above the reeds, poise for an instant to look around her, and dart away. That instant is the collector's only chance. On only one occasion was there a male present when a female was ovipositing; and this, I feel sure, was purely a coincidence.

To the two widely separated records given above, a third was added, August 4th 1938, when Buckell and myself found the species flying at a runway on the Eagle river, some ten miles out of Revelstoke.

On my trip of 1940, I took a single male of *walshii* at Tête Jaune, August 8th. It was flying in the sun, among the trees overlooking a large (quite unworkable) muskeg swamp. This specimen is very small—39 mm. The creeks in the Yellow Pass area are too cold for either *Somatochlora walshii* or *minor*, being of icy cold mountain spring origin, or glacial streams.

Flight period: July 25th to August 18th. Based upon my captures in British Columbia and Alberta, I estimate *walshii* in the west emerges about July 10th, to fly into September.

Map areas: 2, 4, 6, and 9.

Somatochlora minor Calvert

The long stay allotted to Forbes Landing in my 1937 trip up Vancouver Island was intended to determine what further species of the genus *Somatochlora* occurred in that district, for I had taken *albicincta*, *semicircularis* and a single of *walshii* there in my brief visit in 1935 and the argument was all in favour of *minor* also being present could I but find its habitat.

On July 27th, on *walshii's* drainage creek, I caught a male of *minor*, and

on July 29th I saw a female—the conspicuous vulvar lamina obviating the possibility of error. Then, on July 31st, at the same place, I caught both a male and female. But, while I had taken the insect, I had not located its true breeding place: a swifter creek, with clearer water must be found. On August 18th I got out to Miller's creek, which, draining the swamp end of Gooseneck Lake, empties into Snake Lake, some six miles from Upper Campbell Lake. A wonderful dragonfly country! Here I took 7 males and 1 female of *S. minor*. And, just as I had netted the odd *minor* at *walshii's* sluggish ditch, so now I got the odd *walshii* on *minor's* rapid creek. All of which bears out what Walker said as to the breeding habits of these two species in his admirable monograph. In that work, however, he had to show the Province of British Columbia a blank as to these two species, which the requisite amount of collecting has corrected. However, my belief that the above captures constituted the initial record for *minor* in the Province proved to be incorrect, for upon communicating with the Canadian National Collection, Ottawa, I was informed that they had one male specimen, taken by J. McDunnough at Shuswap Lake, (mainland, Kamloops-Revelstoke) July 22nd 1926. I have more recently learned that Buckell also located a habitat of this species in 1937, at Jesmond in the Cariboo, taking 2 males and 1 female. His dates were June 23rd and August 5th. Thus there are three widely separated records, on Vancouver Island, and the mainland south of 52″.

Flight period: June 23rd to August 19th. In spite of the single June record, I estimate the season about the same as that of *S. walshii:* July 10th into September in western Canada.

Map areas: 2, and, northerly, in 4 and 5.

Somatochlora franklini (Selys)

Two collectors, Walker and Buckell, have taken this species in British Columbia south of 52″, the locality being the same: Field. Here it flies with the muskeg *Aeschna, sitchensis,* which I found to be the case in Alberta both at Nordegg and in tamarack swamps west of Red Deer. This, however, appears to be a rule that does not work both ways, for there are innumerable locality records for *sitchensis* in this Province, with no evidence of *franklini.* Southwardly, in western Canada, it favours the Rocky Mountain range.

On my Atlin trip, 1939, (60″ north) I located *franklini* July 14th on a tiny streamlet that drained a large muskeg pool. It ran through a bog, some 50 feet wide, between trees and terminated after a course of 150 yards in a mud pool devoid of life. On that day I netted a male, and a female ovipositing. The insects were mature but still young; that is to say the play period following emerging—when they fly wide of the water—was over, and they were back at their habitat to breed. On that occasion an aged *Aeschna coerulea septentrionalis* female was taken ovipositing, and an *Aeschna sitchensis* female emerging. On July 17th I visited the place again, taking a male *franklini,* and seeing a female; but subsequent visits on July 26th and August 9th were most disappointing, no more being seen.

Flight period: actual captures: July 14th to August 27th. Western records would indicate emergence early July, the flight continuing into early September.

Map areas: 8 and 13 (Atlin).

SOMATOCHLORA SEMICIRCULARIS (Selys)

Walker (1927) gives a number of localities and states this "is by far the commonest and most generally distributed of the genus in British Columbia," and in this I concur. In 1935 I took a ♀ of *semicircularis* at Mud Lake, Forbes Landing, Vancouver Island, August 11th; and a single ♂ on Grouse Mountain, Vancouver, 4,000 feet, August 20th. In 1936, on the mainland, two ♂s were netted at Cultus Lake (runway near Indian Village) July 2nd; and Hope district produced the following locations: Silver Creek Lake, July 27th, three ♂s, 1200 feet; Little Mountain, two ♂s and a pair seen in cop., August 2nd; Texas Lake, three ♂s, August 3rd.

My long collecting trip on Vancouver Island, 1937, served not only further to confirm the general distribution of this species, but to give a better idea as to its period of flight. At Sooke, in the south, the insects were fully adult, in cop. and ovipositing, on June 7th; and on the "Forbidden Plateau," Courtenay district, they were taken in first-class condition August 26th. It would be safe, therefore, to state that on the Island they fly from the end of May to the beginning of September. This is longer than is usually credited to species of the genus, but, to my mind, where the 'flight period' of a given dragonfly is stated to be short (and this applies to most of the rarer species) the belief is based upon insufficient collecting rather than fact.

My records on Vancouver Island, besides the localities already given, were Florence Lake district, junction of Waugh and Goldstream creeks, July 4th; and Forbes Landing district, all suitable water between the Lower and Upper Campbell Lakes July 25th-August 18th. *Semicircularis* seems to prefer reedy swamps, small pools and muskeg pot-holes; but I have taken it on quite large lakes, where these have shallow, reedy shores.

Distribution: localities selected from lists to indicate extent of range: Walker (1927) Prince Rupert, Garibaldi district, Peachland, Glacier, Ainsworth, Bear Creek. Ricker took it at Lost Slough near Cultus Lake. Buckell adds: Chilcotin, Fernie, Field, Moyie, Prince George, Quesnel, Revelstoke, Slocan Park, Stanley, and, in 1937, Jesmond. From my own long list I contribute: Christina Lake.

In 1940 I found this species common at the muskeg end of a long slough at Mount Robson (Yellowhead Pass) August 4th. There was no trace of yellow lateral abdominal spots in these specimens, but segment 8 had whitist apical annulus. It was also quite plentiful at Tête Jaune, August 11th, at the marshy sloughs along the railway tracks.

Flight period: June 7th to August 26th.

Map areas: 1-11. I failed to locate this species at Atlin, but there are two records in Alaska (Gloyd 1939).

Somatochlora whitehousei E. M. Walker

Walker (1927) gives one record for this species in British Columbia: a single specimen taken by P. N. Vroom on Revelstoke Mountain, 6,000 ft., August 12th, 1923. Accompanied by Buckell, I visited the muskeg pools in question August 3rd, 1938, but *Somatochlora semicircularis* only was to be seen. Buckell, however, had taken a single male of *whitehousei*, July 7th of the previous year at Jesmond, in the Cariboo; the location being the series of muskeg pools above the dam. At the dam itself he captured a number of *Somatochlora hudsonica* and three *S. minor*. It is a wonderful location for this genus, combining the requirements of all: lake, muskeg, flowing creek and stagnant brook, but it was too late (4th week of August) when I visited in 1938. The midsummer fliers were over—the fall brood on the wing!

Flight period: actual captures July 7th and August 12th. Walker (1927) gives: June 12th to August 15th.

May areas: 4 and 6.

Somatochlora septentrionalis (Hagen)

On my Atlin trip (1939) the first specimen taken was a male of this species, July 6th. The insect was flying at a small muskeg pool, of some 25 feet diameter. The total series from that date to July 22nd consisted of 14 males and 6 females; with a further belated female on August 21st. I had tried to catch her on August 6th and again on August 8th, as she flew with the apical third of her abdomen drooped at a right angle, but without success. From July 22nd to August 5th the weather had been cold, windy and sunless, with frost on the night of August 3rd. Previously, the only record for British Columbia was a single male in the Provincial Museum, Victoria: "Atlin, July 20th, 1914": Walker (1927).

In fresh male specimens segments 6, 7, 8 and 9, have faint whitish apical annuli: the last two plainly discernable, that of 7 less so, and that of 6 scarcely perceptible. Seg. 10, dorsal view, is polished black, in striking contrast to the metallic blackish green of segments 3-9. In the female, segments 6 to 10 have similar whitish apical annuli, grading off as in the male. Seg. 10 is metallic blackish green, and not black as in the male. In the final female taken, I noted particularly that she had small basal lateral dull yellow spots on segments 5, 6 and 7.

Ovipositing is performed in the centre of the pool, with a deliberate dip, dip, dip, of the tip of the abdomen, whilst the insect moves around in alert flight. She is indifferent as to whether the eggs go into clear water, or into the creamy-pink slime of decayed vegetation arising in places to the surface. For her task, she appears (apparently from nowhere) well in the middle of the pool, and, once this is completed, she leaves it, unobtrusively as she came, and usually on the side remote from the collector. I have witnessed this over and over again, and my scanty captures indicate the dif-

ficulty of netting this sex. I followed one female 100 feet back from the water, as she flew low selecting a place to alight with nice discrimination: her choice being a small pot-hole, surrounded with tall grass. Unable to see her, but positive that she was there, I placed my large kite-net on top, and she flew up into it. On another occasion I followed a male, and netted him in precisely the same way. I feel sure that such small grass-ringed pot-holes are the natural resting place of this species; for to fly back to the trees in a large muskeg flat would be too far from their water, and the scrub willow of the muskeg would offer no protection from the ever prevailing wind of northern latitudes. Indeed, at the extreme northern limit of its range (and higher altitude habitats) there would be no trees.

Ovipositing: the males hawk over the pools awaiting mates, and they are slightly less cautious in approaching the edge. They will hover momentarily on occasion, but restless flight is more usual. More than one on a pool at the same time is rare. The female is seized over the water, and they fly back over the muskeg and scrub willow: presumably to come to rest in a pot-hole as described in the case of individuals. In about fifteen minutes she is back ovipositing; and her male (should he return) while taking no interest in the proceedings, will not interfere with her.

The habitat of this species is small muskeg pools of 25 to 50 feet in length, with level wet edges, as favored by *Aeschna c. septentrionalis,* not large muskeg pools, with firm peaty banks, where *Somatochlora albicincta* and *hudsonica* fly. In the case of *A. c. septentrionalis* I have given the reason for this, viz, ovipositing requirements, but another must be found for *S. septentrionalis,* since it oviposits in the middle of the pool. Two solutions are available: (a) that nymphal life demands the rather shallower water of the smaller pools, and the creamy-pink slime of decayed vegetation peculiar to them; or (b) that at the smaller pools the females can oviposit in peace, undisturbed by the annoying attentions of the larger white-ringed species. In support of the latter argument, I may say that only once did I see an individual of this species on the large pool—a female striving to oviposit. She was driven off by males of *S. albicincta* and *S. hudsonica,* and, returning, was driven off again. She did not return.

The nymph of *S. septentrionalis* being unknown, I spent the cloudy days of July 10th and 11th hunting for exuviae, gathering all that I could find around the four pools where the species had been flying on the previous sunny day, and rejoicing in those found of measurement around 21 mm.—the length of the nymph of *S. whitehousei*—the nearest ally. In view of Dr. E. M. Walker's oustanding knowledge of the genus, I sent my total find to him. He classified 9 exuviae as of this species; his description being as follows:

Nymph (final exuvia, Figs. 5-7); pale brownish or almost colourless, the only distinct markings being those of the abdominal segments, most of which are marked on each side with a pair of darker brown lateral spots

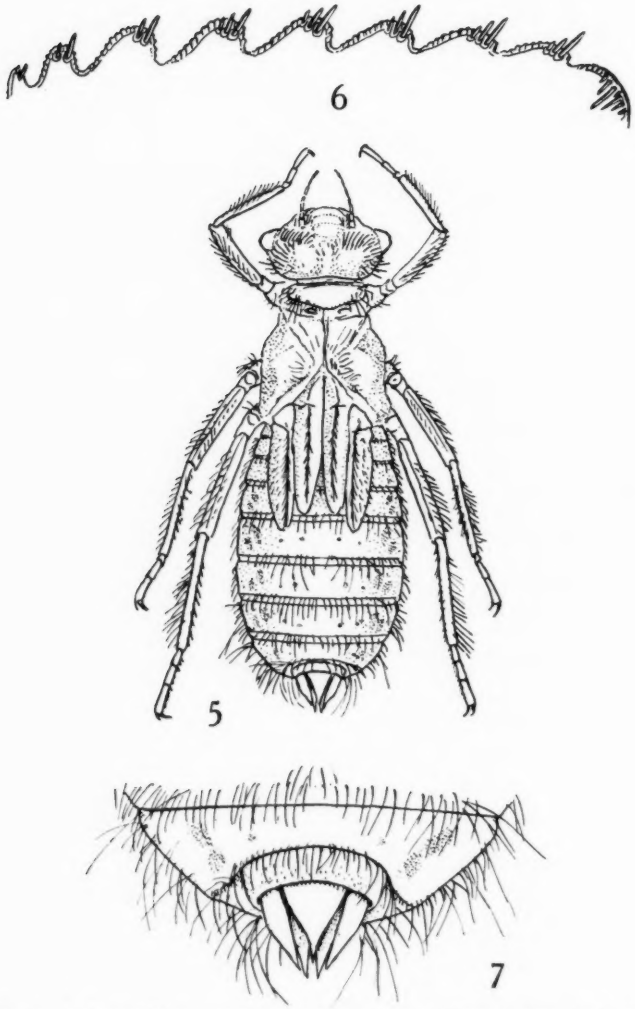


PLATE 2. *Somatochlora septentrionalis* Hagen. Fig. 5. Nymph, from final exuvia, ♂. Fig. 6. Crenulations of labial palpus. Fig. 7. Terminal segments and caudal pyramid, dorsal view.

(muscle scars) and two pairs of dark dorsal puncta, those nearer the median line being larger.

Eyes as in *whitehousei*, less prominent than in the *arctica* group; postocular margins of head passing in a broad curve into the hind margin, which is but little concave; a patch of rather long hairs on dorsal surface of head next to the eyes and along lateral margin; antennae nearly bare. Labium large, the mentum broader than long, reaching laterad as far as inner margin of eyes (as viewed from below); mental setae 11-13, usually 12, the 3rd to 8th from outside being longest, the 4 or 5 innermost much smaller than the others; a few marginal mental spinules, including 3 or 4 at the articulation; labial palpi with about 8 deeply-cut crenulations (Fig. 6) each typically with 3 setae in a graded series, the longest about equal to the height of one of the crenulations; lateral setae usually 8, the first smaller than the others, more rarely 7.

Pronotum with antero-lateral angles somewhat acute and elevated, with a tuft of hairs. Legs very hairy, hind femora reaching to about the middle of segment 6; wing-pads reaching just over the base of 6, the costal margin of each pad with a row of hairs, those of the hind wing much the longer; hind wings also with some additional hairs along some of the longitudinal veins.

Abdomen elliptical, nearly twice as long as broad, its greatest breadth at segments 5-6, abruptly narrowing on 9, without trace of lateral spines or dorsal hooks. Hairs of dorsal surface small and scattered except along hind margins of segments, those on segments 5 to 9 being increasingly longer, some of them being as long as the segments which follow them; lateral margins of most of the segments also with a fringe of hairs, which is very long on the last 3 segments.

Caudal pyramid somewhat longer than segments 9 and 10; median appendage about as long as broad, slightly acuminate, lateral appendages of about same length as median, outer margin in male slightly bent, in female straighter; inner margin in male straight, in female somewhat convex, apices acute; inferior appendages slightly longer than the other appendages, straight, regularly tapering to acute apices.

Length (mm.) 19-20, abdomen 11-12, hind wing 6-6.5, hind femur 5.7-6, width of head 6, width of abdomen 6.5-7.

Described from nine exuviae, all more or less damaged. They were heavily coated with a greyish deposit and had to be soaked in water and cleaned before they could be studied. The cleaning was facilitated by placing them in dilute hydrochloric acid, which produced a vigorous bubbling but still left a heavy residue. (A similar deposit coated the exuviae of *S. whitehousei* which the writer found in a springy bog at Banff, Alberta.)

The nymph of *S. septentrionalis* is extremely like that of *S. whitehousei*, differing chiefly in the presence of abdominal markings, which are absent in

the latter species, and in the larger number of mental and lateral setae of the labium, which in *whitehousei* are 9 or 10 and 6 or 7 (rarely 8) respectively. These two closely related species are the only ones in North America in which there are no traces of lateral spines on segment 9. The same character is found in the Eurasian species of this group, *S. alpestris*. (E. M. Walker)

Flight period: Actual captures July 6th to August 21st. Emergence must have commenced two or three weeks earlier, so its full season would be (as might be expected) similar to *S. whitehousei*, say June 15th to the 4th week in August.

Map areas: 13, Atlin, at extreme north.

SOMATOCHLORA ALBICINCTA (Burm.)

In western Canada—British Columbia and Albertan Rocky Mountains—three forms of *albicincta* occur, and these should be considered separately where the distribution of the species is concerned.

(a) The typical small northern form, a Hudsonian zone species. I took a number at Nordegg, Alberta, in July 1917, and Walker (1927) records it from Banff. It will doubtless be taken on the western slope of the Rocky Mountains in British Columbia, and in its true habitat northerly in the Province. Specimens taken by me, 1937, on the "Forbidden Plateau" (3,200 ft.) Courtenay V.I. are quite small: date August 26th.

(b) A larger form than (a), and, as Walker states in his paper, "darker, with somewhat less conspicuous white annuli." This is the common form in British Columbia, generally speaking, south of and at lower altitude than the true habitat.

My records for this form are, mainland: Grouse Mountain, Vancouver, August 20th; Hope district, Kawakawa Lake, July 28th-August 5th; Little Mountain, August 1st; Harrison Bay district, Echo Lake, August 10th, Elbow Lake, August 12th, Squawcum Lake, August 19th, a ♂ netted and a ♀ ovipositing. Vancouver Island: Forbes Landing, (Mud Lake) August 9th, but, as to this last record, see what is said under (c).

(c) This form, for which I suggest the name *massettensis*, is of very large size: on the wing, both as to length and width across the abdomen at segment 5, having the appearance of *Somatochlora cingulata*. Length, overall, 58 mm. Wing-spread 79 mm.

I found young females flying at a runway some miles east of Massett, Graham Island, Queen Charlotte Islands, July 20th-23rd, 1935. The exact locality was James Pearson's pasture, separated from the great north beach only by sand dunes, surmounted by a fringe of conifers. The insects were hawking for flies, then resting high on the trees in the sun. From below I was struck by the way the appendages were carried in flight at a wide angle. I secured two females, but unfortunately missed two other chances, and no

male was taken. This is evidently a northern, sea level form; and I do not doubt that in August a good series might be obtained.

The three weeks spent at Forbes Landing, Vancouver Island, July 25 to August 18th 1937, permitted further study of *albicincta* as flying there. On the first date mentioned I took a male and female of recent emergence; and between August 8th and 18th I netted males and ovipositing females both at Mud Lake and at the mouth of the drainage creek between Lower Campbell Lake and McIroy's Lake. This flows either way according to the levels of the respective lakes at different seasons. This series is of considerable interest, for whereas the males are approximately form (b) the females are oversized and qualify for form (c) *massettensis*. Further, it should be noted, that at Massett, Q.C. Is., I failed to secure males, so I do not know if they are oversize like the females, or relatively smaller as in the Forbes Landing insects.

Distribution: On my 1938 trip, I took a female at Peachland (Trepanier creek) July 23rd, and a female, ovipositing, at Field (Narao Lake—5,610 feet) August 11th. Also, with Buckell, a long series—very small size—at the top of Revelstoke Mountain, 6,300 feet, August 3rd. Walker (1927) records Nanaimo district, Black Tusk mountains, Garibaldi district and Bear Lake. Ricker took it at sloughs and lakes, Liumchin Mountain. And Buckell adds: Falkland, (Arthur Lake) and Salmon Arm (Fish Lake).

On my trip of 1939 to Atlin, B.C., (60″ north) I located typical *albicincta* on July 6th flying with *Somatochlora hudsonica* in about equal numbers, though I feel sure that those of the latter species were of earlier emergence. Subsequently I found *albicincta* on a number of pools throughout July and August: my last record being August 29th, a female ovipositing and 3 males. Nothing had been seen of *S. hudsonica* since July 22nd.

Flight period: June 30th to August 29th. But my Atlin captures, of July 6th, had most certainly emerged at least ten days earlier: so the season in this Province might be stated as June 25th to the end of August.

Map areas: 1-6, 12 (form c) and 13. Alaska, Gloyd 1939.

Somatochlora hudsonica (Hagen)

At the date of Walker's paper (1927) he could publish no record for this species in British Columbia. Since then Buckell has taken it at no less than six localities south of 54″, viz., Falkland (Arthur Lake), Kamloops (Lac le Jeune) Salmon Arm, Bridge Lake, Jesmond and Prince George (Summit Lake).

At Atlin, July 6th 1939 (60″ north) I found *hudsonica* at its true habitat: a muskeg pool with a firm peaty edge. It was flying with its ally and usual companion, *Somatochlora albicincta*, in about equal numbers. On that date I took 5 males, and 2 females ovipositing; and subsequent visits to the pool increased my series to 13 males and 6 females. The last netted was a male on

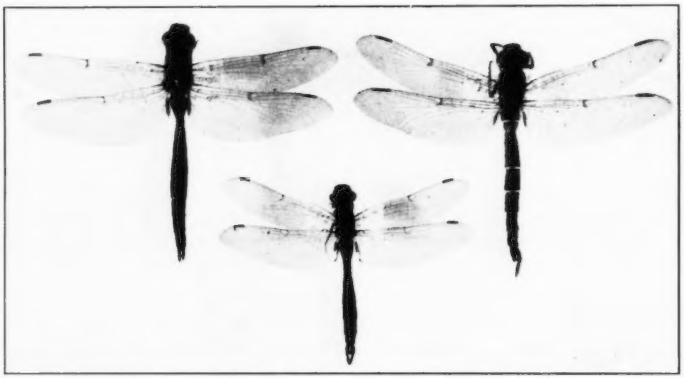
July 22nd. These were the first *hudsonica* I had taken since I first found the species in Alberta back in 1916.

S. hudsonica is an easy species to net since the females oviposit around the edge of the pool, and the males patrol the shore line close in looking for them. A pair in copula flies back into the trees. On July 12th I netted a pair over the water struggling to make connection of which the female was *S. hudsonica* and the male *S. albicincta;* and I imagine such abortive attempts between these species must be of fairly common occurrence. The fact remains, however, that one never takes a specimen even remotely suggestive of hybridism. On the wing the slightly larger size of the *hudsonica* male serves to separate it from *albicincta;* and with the females identification is still easier: that of the former being distinctly more robust.

On my trip of 1940, I found *hudsonica* at only one place between Prince Rupert and the Alberta border, viz., Burns Lake. Here, at two large sloughs it was very common, June 29th to July 7th. They varied considerably in size and I caught and reelased many individuals in expectation of finding *Somatochlora albicincta,* its usual flying mate, but without success. Next to *semicircularis* the species last mentioned is the commonest insect of the genus in the Province, yet, in over two months I found no single habitat.

Flight period: June 29th to August 27th. Where this species and *S. albicincta* occur at the same habitat (as at Atlin, July 6th) the state of maturity of the insects and oviposition lead to the view that *hudsonica* is of rather earlier emergence. I should estimate the date about June 12th to 15th.

Map areas: 4 (northerly) 5, 10 and 13. Alaska, Fort Yukon, Walker (1925), Gloyd (1939).



Left to right: reduced one-third, *S. albicincta,* form *massettensis,* sea shore, Massett, Queen Charlotte Islands. *S. albicincta,* typical, Revelstoke Mt., 6,300 ft., 200 miles south of Massett. *S. cingulata,* typical, to show comparative sizes.

Somatochlora cingulata (Selys)

Credit for the first record for *cingulata* in British Columbia falls to Buckell, he having found it, August 10th, 1932, at Arthur Lake, Falkland, in the Okanagan Valley. This location gave the required conditions: a fairly large lake at a fairly high altitude, 4,000 ft. A series of ten was taken. The two allied, white-belted, species: *Somatochlora hudsonica* and *albicincta*, were also present.

Flight period: only collecting date, August 10th. In the Alberta Rockies I took tenerals of this species July 14th and 17th; and, based upon these and other records, both western and eastern, I judge its season to be rather later than that of *S. albicincta:* say the 4th week of June to early in September.

Map areas: 5 (mountain lake, 4,000 ft.).

Libellulidae

Libellula julia Uhler

This is the most subdued species of the genus flying in the Province. The males rest on water lilies and reeds, with occasional short flights, and the females oviposit quietly among the reeds without their fertilizing males being in evidence.

Walker's records are restricted to south Vancouver Island, which I can extend northwardly to Northey's Lake, Courtenay, August 13th; and Mud Lake, Forbes Landing, August 10th. My 1936 trip also established *julia* as a mainland species, the records being one ♂ Chilliwack, July 21st; four ♂s and five ♀s Kawakawa Lake, Hope, July 28th-August 5th; and several ♂s Echo Lake, Harrison Bay, August 10th-23rd. By the last date given the insects were aged.

My three months' trip on Vancouver Island in 1937 supplied records for this species at every body of water visited from Sooke, in the extreme south, June 12th—they were then mature and plentiful—to Upper Campbell Lake, in the north. My last date is Courtenay, August 26th, and I have a notation: "still in good condition." The species, away from the water, rests on roadways, rocks and shrubs indiscriminately.

Distribution, mainland: I found *julia* abundant at Christina Lake, July 1st-15th 1938; and Buckell records it from Osoyoos and Oliver in the south, to Salmon Arm (Loon Lake) and Horsefly in the north. The last locality is north of 52″.

Flight period: June 12th to August 26th.

Map areas: 1, 2, 4, 5, 6 and 10.

Libellula quadrimaculata Linné

This species is so generally distributed in the Province (including the Queen Charlotte Islands) that I feel justified in omitting my lengthy records

for both the mainland and Vancouver Island, and to state instead, most bodies of water inhabited by dragonflies. It should also be remarked that it is on the wing from early May to the end of September. In point of fact, *quadrimaculata* is frequently a great nuisance to the collector, in preventing the capture of a rarer insect by rushing at it at the critical moment.

In my paper (1917) I mentioned the habit of males of this species standing by while their females were ovipositing. The summer of 1936 at Texas Lake, Hope, I watched two pairs so disporting themselves at a pot-hole sheltered by reeds from the wind on the main lake. Three times females of *Somatochlora semicircularis*, (with no male in attendance, of course) sought to oviposit in the same sanctuary, but were driven off by the guards.

A savage feeder: teneral sympetrums are not infrequently the victim.

All Walker's (1927) records for Vancouver Island for this species relate to the Nanaimo district with three exceptions. In 1937 I found it generally distributed, and I will add: Sooke, June 7th; Thetis Lakes, June 14th; Florence Lake, June 29th to July 4th; and, in the north, Upper Campbell Lake, August 11th, and Courtenay, August 26th. While seen on most bodies of water visited, it must, as to numbers, take second place to *Libellula julia*.

Mainland: (selected) I have records: Vancouver district, Cultus Lake, Chilliwack, Harrison Bay, Hope, Christina Lake, Kaslo, and Crawford Bay --Kootenay Lake district. Ricker contributes: Sumas Canal, Liumchin creek. And of Buckell's list: Chilcotin, Clinton, Edgewater, Horsefly, Osoyoos, Princeton, Revelstoke, Salmon Arm, Westbank. Walker (1927) Prince Rupert, Cranbrook. J. Wynne, Enderby, May 24th.

On my trip of 1940, Prince Rupert to the Alberta border, I took this species at Terrace, June 17th; Smithers, June 22nd; Burns Lake, June 29th and McBride, July 12th. It was the only species of the genus seen throughout the Summer.

Flight period: May 7th to September 29th.

Map areas: 1-12. At Atlin (north in area 13) I failed to find this species, but Mrs. Gloyd's Alaskan list (1939) supplies two records.

Libellula pulchella Drury

At the time of Walker's (1927) paper the only record for *pulchella* was his own at Penticton. Since then Buckell's work in the Okanagan Valley section has extended its range from Osoyoos (on the international border) northward through Oliver, Peachland, Vernon to Salmon Arm. He has also a somewhat unexpected record of Revelstoke, since this is out of the Sonoran—dry Transition zonal area to which the species obviously belongs in this Province.

I took a nice series of *pulchella* around a large marsh at Penticton, July 15th to 18th, 1938, where *Libellula forensis* was also abundant. If I found it difficult sorting out on the wing those I desired, the insects themselves

appeared to be in no better state, for they chased individuals of the allied species into the air as often as their own. Confusion reigned. These two striking dragonflies were surely never intended to fly together!

Flight period: (actual records) June 9th to August 20th. The full season for this species is doubtless very similar to that of its close ally (and flying mate at Penticton) *L. forensis:* the first week of June, well into September.

Map areas: 5 and 6.

Note: for association of these species in Oregon, Nevada and California, see Kennedy (1915, 1917).

Libellula forensis Hagen

Needham states that this species is "the western equivalent of *L. pulchella*" which while broadly speaking is correct, is not precisely so, for Walker (1927) found them flying together at Penticton. Over how wide an area they overlap has not been determined. (See Note, *pulchella*).

Forensis, a species of long flight period and wide distribution, must give place to *Libellula quadrimaculata* in both respects, nor is it, to my experience, as common: though, owing to its size and beauty, it is conspicuous wherever it occurs. It is true of many of the *Anisoptera* (or appears to be) that the males are more numerous than the females, and this is particularly the case with this insect: of which I netted and released scores of males before obtaining a short series of females for my own requirements.

The sturdy nymph is willing on occasion to travel well back from the water to transform. I took one at Beaver Lake, Vancouver, on June 27th 1935, at 10 a. m., scrambling across the path in full sunshine, and making good time of it.

On Vancouver Island *forensis* occurs quite widely and my 1937 records extend from Sooke, in the south, June 12th, to the Upper and Lower Campbell Lakes, in the north, July 25th-August 18th. In the Nanaimo district: Wellington Lakes, Newcastle Island, etc. it is very plentiful, but I cannot concur with Walker's statement (1927) "the commonest *Libellula* of southwestern British Columbia." On the Island, over a wide area, *julia*, I feel sure, exceeds it. On the mainland, I have records: Cultus Lake, June 19th; Chilliwack golf course slough, July 17th, Hope district, July 28th-August 2nd, Hatzic Lake, August 7th, Harrison Bay, August 10th, all 1936; Kaslo, June 21st, Christina Lake, July 4th-5th, Penticton, July 15th-23rd 1938. Buckell contributes: Salmon Arm, Oliver and Osoyoos.

Flight period: June 3rd to September 16th.

Map areas: 1-7.

Libellula lydia Drury

This attractive species, in which the sexes differ, (Howard's fig. 1, plate XL, is of course a young ♂) is of wide distribution in the Province, my

records extending as far north as Forbes Landing, Vancouver Island; and, on the mainland, from Vancouver to the Hope-Princeton trail, one hundred and twelve miles east.

The male poises on the wing over his ovipositing female and drives away all intruders, but whereas *L. quadrimaculata* distributes her eggs within a limited area, *lydia* will remain hovering, or settled, at one spot, driving her abdomen dozens of times into the algae beneath.

On Vancouver Island *lydia* is the least common *Libellula*, though as widely distributed according to the available data. My 1937 locality records were: Sooke, 2 or 3 seen, June 7th; Thetis Lake, 1 seen, June 20th; Long Lake, fairly common, June 25th; Florence Lake, not common, June 29th-July 4th; Nanaimo district: Wellington Lakes, a few seen, July 14th, and Newcastle Island, a male and female seen July 16th. Courtenay, 2 seen, July 20th; Forbes Landing district, a few seen, July 25th-August 18th. At Vancouver, Beaver Lake, Stanley Park, *lydia* swarms the last week in June—the heights of its season. On June 27th, 1935, I counted ten males resting on the path within an area of a few feet, and I have seen as many on one long garden seat.

Distribution: omitting Walker's (1927) Vancouver Island records, as my own given above suffice, his mainland locations are: Cloverdale and Rosedale (Blackmore) and Boundary (Bruce). Ricker has taken it at Cultus Lake and Vedder Crossing; and Buckell at Oliver and Osoyoos. My record at Forbes Landing, Vancouver Island, is on 52″, but the mainland ones are spread along the international border.

Flight period: May 14th to September 24th.

Map areas: 1-6. (The last by virtue of the record "Boundary," [Walker 1927] a name applied to the district, Grand Forks-Cascade, on the international border).

ERYTHEMIS SIMPLICICOLLIS (race COLLOCATA) Hagen

Walker has satisfied himself that the British Columbian insect differs slightly as to segment 3 from the eastern *simplicicollis* (thus supporting the view of the late E. B. Williamson) but not to an extent justifying specific rank: I, therefore, list it as race *collocata*.

With seven weeks of my Vancouver Island trip of 1937 allotted to the southern area, I had anticipated taking a good series of this insect, but in this I was disappointed. My captures were: roadway between Pike and Long Lakes (of the Thetis group) 2 females, June 25th and another June 27th. Shore of Long Lake, pair in cop., June 27th. Goldstream, reservoir road, a young male, July 4th; pot-hole, near Florence Lake, a female ovipositing, July 5th; and Newcastle Island pond, one seen, July 16th, flying with *Pachydiplax longipennis* and *Sympetrum illotum*. The insect is given to resting on

gravelly roads, after the manner of species of the genus *Ophiogomphus*, *Leucorrhinia* etc.

This species has cross-veins below the stigma, but no brown stain at the base of the wings; whereas *P. longipennis* has the base of the wings stained, but no cross-veins below the stigma. These points are worth remembering in the field, as pruinose males are otherwise much alike.

Early July 1941, a teneral ♀ was taken on a lawn in Vancouver; and, collecting at Chilliwack, July 24th and 25th 1941, I found the insect flying, in association with *Leucorrhinia intacta*, at the large slough near the old golf course: 3 ♂s and 1 ♀ being netted. Chilliwack is some 70 miles east of Vancouver, and the belief of Walker and myself that the species was confined in British Columbia to the south end of Vancouver Island is clearly incorrect.

At Chilliwack a female was observed ovipositing, and not only was this similar to the egg-laying of *Leucorrhinia intacta*, but her tactics, to avoid further attention from the hovering male, were precisely as described by me under that species.

Flight period, records June 1st to July 25th.

Map areas: 1, 3 and 4.

Pachydiplax longipennis (Burm.)

As in the case of the preceding insect, this species proved somewhat disappointing in my Vancouver Island trip of 1937, when, though in its recorded territory from June 4th to July 16th, I took it at but two localities: the junction of Waugh and Goldstream creeks, a young male, July 4th; and the pond on Newcastle Island (off Nanaimo) July 16th, 12 males.

Except as to colour, this species and *Sympetrum illotum* are much alike in form, and in behaviour they appear identical. They both delight in perching, with wings drooped, at the extreme tip of a dry twig; from which point of vantage they make short sallies to catch a fly or to rush at any other species invading their chosen territory. They are both given to hovering, and are thus easy to net.

Flight period: records, June 30th to July 23rd. These dates represent too short a span for its full season.

Map areas: 1. Walker (1927) gives a record for Vancouver, which he credits to Osburn. This I think was in error, for I failed to find the record in Osburn's paper (1905); and I most certainly have never found the species in the Vancouver district during six years of residence.

Sympetrum illotum (Hagen)

On June 21st 1935, at Beaver Lake, Stanley Park, Vancouver, I saw a fly of this species, and on the following day at the same spot I netted a male:

possibly the same insect. This to date is the only record on the mainland of Canada. The breeding place, since discovered, is the pond adjoining the reservoir, Stanley Park.

For Vancouver Island, my trip of 1937 provided additional locality records as follows: Sooke, flying with *Ischnura erratica, Somatochlora semicircularis,* etc., 3 males, June 7th; Thetis Lake group: Long Lake, 4 pairs in cop netted and singles, June 25th and 27th; Florence Lake, a few seen, June 29th-July 4th; and, at a large slough nearby (another breeding place) a good series taken. Nanaimo district: Rock City pond, July 8th, and Newcastle Island, fairly common and flying in cop., July 16th. My next moves were north to Courtenay and Forbes Landing, and no more of the species were seen. Walker (1927) records dates as late as August 14th; and the argument is that I had moved out of *illotum's* range. It was the same with *Sym. madidum,* and it tends to strengthen my convictions as to a change in zone, as discussed under *Lestes disjunctus.*

The resting habits of this species are referred to under *Pachydiplax longipennis.* Ovipositing was observed upon a number of occasions: the pair usually arrive at the water flying tandem, and the eggs are dipped in, an inch or so apart, where open spaces occur between the reeds. The male not infrequently tires of his share in the proceedings (purely ornamental!) and relinquishes his grasp, when the female (better informed as to the supply of eggs demanding release than he) continues her duties alone. What more striking contrast in nature than a number of bright scarlet *illotum* flying over green reeds!

Flight period: records, May 20th to August 14th.

Map areas: 1 (common) and 3 (Stanley Park, Vancouver, rare).

Sympetrum corruptum (Hagen)

Previous records in the Province have been interior districts: Okanagan and West Kootenay, and, north of these, on the main line of the Canadian Pacific Railway. June 14th 1936, I took a young male at Stanley Park reservoir, Vancouver; and the same season netted single specimens at Hope, July 29th, and Harrison Bay, August 10th. At Hatzic Lake, August 8th, I captured and saw enough tenerals to cause the notation: "apparently common here," and this I should the more readily make since it was the first time that I had personally ever found it common anywhere.

This is one of the species that for some unaccountable reason is usually noted when teneral. Of course the "motley" of the young insects instantly catches the eye, whereas adults might be overlooked in the galaxy of red forms on the wing together in this Province. Such explanation, however, is unsatisfying, and it is more likely the case that whereas one may come across ranging young insects anywhere, to take adults needs locating their breeding place when they re-assemble for that purpose.

Above I referred to a general emergence of *corruptum* at Hatzic Lake the first week in August 1936. At Kaslo, 1938, I found a general emergence taking place the first week in June. If, as would appear from this, the insect is double-brooded, with an interval of two months, it is understandable why occasional specimens are taken throughout the season, from early June to well into September. In my Alberta paper (1917) I expressed perplexity over this. It would seem that I have now answered my own riddle.

Distribution: Walker (1927) records: Penticton, Peachland, Nelson, and gives dates June 7th to September 13th; and (1938) Cultus Lake, August 26th, Chilliwack Golf Course, August 11th. Buckell contributes: Cranbrook, Creston, Hope, Kamloops, Oliver, Osoyoos and Wasa. J. Wynne, Enderby, teneral female, June 4th.

Flight period: First brood 1st week in June; second brood last week in July and 1st week in August: flying until September 13th.

Map areas: records, 3, 4, 5, 7 and 8.

Sympetrum madidum (Hagen)

All Walker's records of this species in British Columbia relate to Vancouver Island. In 1936, however, I took three ♂s at a small pond on the Chilliwack golf course, the dates being July 22nd-23rd; and on August 2nd a ♂ in a dry stony runway on the Hope-Princeton trail, some twelve miles east of Hope.

The even-textured red wings make the insect conspicuous to the collector.

On Vancouver Island, as early as June 7th, I took a young male of *madidum* at Sooke. This was on *Ischnura erratica's* reedy pool, and where tenerals of the Sympetrum were emerging. Florence Lake (at a nearby pot-hole) a number of adults were flying and a pair in cop., July 5th. Nanaimo district: Departure Bay, 1 netted and another seen, July 8th, and Wellington Lakes, 4 pairs in cop., July 14th-15th. North of here none were taken or seen. Whether it is due to this species favouring particularly foul water breeding places or other cause I do not know, but my specimens were usually heavily laden with red mites.

Distribution: Walker (1927) records Nicola Lake, July 26th. Buckell (1938) gives Aspen Grove, Bridge Lake, Canim Lake, Hat Creek, 70-Mile House, Osoyoos, Princeton, Salmon Arm, Tatla Lake; and since then at Jesmond, Kamloops and 100-Mile House.

Flight period: June 7th to September 7th.

Map areas: 1, 2, 4, 5, and 10 (southerly).

Sympetrum costiferum (Hagen)

Most authors in describing this species feature the flavescence of the costal margin, irrespective of sex. Admittedly this should be so or Hagen's

name for the insect is misleading, but the fact remains that it is only true of tenerals. According to my experience, in fully mature red males the tinge of colour along the costa is scarcely discernible. Mature females, on the contrary, may have wings flooded with colour, intense as to the upper half and fading away to the lower margins.

In western Canada, with the exception of *vicinum*, *costiferum* is the last of the genus to appear. My 1935 notes record teneral ♂ and ♀ August 10th and 11th, at Forbes Landing, Vancouver Island; and, 1936, tenerals emerging August 8th at Hatzic Lake. The first records in my Alberta list (1918) are August 5th and 6th. But it is not until September that the fully mature specimens, discussed in the preceding paragraph, have been noted by me, and I have taken specimens to November 1st. Should this belated maturity be more or less the case elsewhere, it would serve to explain the teneral coloration being stressed in published descriptions: indeed, in view of the name selected, it raises doubts as to the full maturity of Hagen's types. Should this be so, then that author's *S. atripes* might well be fully mature *costiferum*.

The male usually accompanies the female when ovipositing. They delight in resting on earth paths, where these are available near their habitat.

My trip of 1937 on Vancouver Island did not add materially to my data respecting *costiferum*, for I was north of its appearance in Nanaimo district and southwardly. At Forbes Landing it was "emerging in numbers" August 15th, 16th, or five days later than in 1935. This might be attributable to cold, wet weather. Taking Walker's (1927) locality records in conjunction with my own, it is clearly distributed from Victoria to Forbes Landing—and, doubtless, still farther north.

On the mainland, paralleling the international border, locality records for *costiferum* (other collectors' and my own) are virtually continuous from Vancouver to Creston (East Kootenay), which includes areas of both Canadian and Transition zones. Farther north (again using all available records) the species has been taken at Golden, Kamloops, and Crawford Bay (F.C.W.) Brisco, Invermere, Salmon Arm, etc., west to Clinton (Buckell). It would seem of general distribution south of 51″.

In 1940, at Tête Jaune, Lat. 53 N., tenerals were quite numerous August 8th to 12th. This habitat, at the entrance to the Yellowhead Pass, is the most northerly of which I have record in the Province.

Flight period: records, July 8th to October 19th. In Stanley Park, Vancouver, I took a ♀ in good condition November 1st 1936.

Map areas: 1-9. In view of my Tête Jaune captures, I feel sure the species must occur in area 10, at least southerly.

Sympetrum vicinum (Hagen)

The male of this well-named, friendly species is easily recognized among the number of red forms flying together by its lighter tint: scarlet.

At Beaver Lake, Vancouver, from mid-September to the end of October (in spite of nights of several degrees of frost) hundreds of pairs may be seen ovipositing in the wet moss round the shore line, the continual tap, tap, tap of the female organ being admirable in steadfastness of purpose.

I have an early record, teneral ♂, of July 31st, 1936, Hope, and the emergence takes place from then on, with the peak of the flight not until six weeks later, as stated above. In all probability the species is of wide distribution in the Province, but the activity of the collector in the field is pretty well over and he is homeward bent before the general flight is on: hence the somewhat scanty locality records.

For the reason stated above *vicinum* was hardly to be expected southwardly on Vancouver Island, during my 1937 trip up the country. Northerly, at Forbes Landing, it appeared just before I left, August 17th. Walker (1927) gives records Nanaimo district and farther south.

On the mainland: Walker (1938) records, Cultus Lake (Sweltzer Creek) and Chilliwack Golf Course, August 15th, a pair, very teneral.

Flight period: records, July 20th to November 1st.

Map areas: 1-4.

Sympetrum semicinctum (Say)

While the Harrison Bay district (its smaller lakes and streams) yielded a fine variety of dragonflies, the great body of water itself seemed in mid-August to be favoured only by *semicinctum*, which positively swarmed in mated pairs, busy ovipositing. The species is subject to considerable latitude as to size and also as to the density of the wing coloration. Length up to 37 mm., and wingspread to 59 mm.

I have taken tenerals from July 24th, and belated adults to October 10th, but the peak of the flight is, as indicated above, mid-August.

Distribution: my records, mainland, Vancouver to Chilliwack and Harrison Bay, and again Crawford Bay, Kootenay Lake. By filling in with Walker's records, we have a fairly continuous known territory of from the coast to the Selkirk range. On Vancouver Island, Walker (1927) records Nanaimo district and Langford Lake.

Further mainland records: Walker (1927) Armstrong, Peachland, Penticton and Okanagan Landing, and (1938) Cultus Lake and Rosedale. Golden, abundant, August 14th (F.C.W.) Buckell (1938) gives 19 localities, from Field and other points on the eastern boundary, to Clinton in the Cariboo, and south to Osoyoos.

Flight period: July 18th to October 8th.

Map areas. 1, 3-8.

Sympetrum danae (Sulzer)

This species—*S. scoticum* Donovan of my Alberta lists—was emerging at sea level in the Massett district, Queen Charlotte Islands, July 24th-26th, 1935. At Beaver Lake, Stanley Park, Vancouver, I have taken it, occasionally, from September 3rd to October 10th. My other mainland records include Hope (Little Mountain) August 1st, 1936; and Crawford Bay, West Kootenay, mid-August, 1928, where it was plentiful. Also Field, Golden, Revelstoke, Kamloops, and north to Jesmond.

Walker (1927) gives no record for *danae* on Vancouver Island, but on my 1937 trip I anticipated taking it northwardly in view of its numbers on the Queen Charlottes. In this I was not disappointed—but by a very narrow margin. At Forbes Landing the species did not appear until August 17th, and these quite teneral. An adult female was netted at Miller's creek, August 18th. On August 22nd I turned south.

Further mainland distribution: Walker (1927) gives Metlakatla, Quesnel Forks, Okanagan Landing, Cranbrook; and, (1938) Hope Slough and Rosedale. Buckell contributes 28 localities, from Osoyoos, on the international border, to Prince George (Summit Lake) and from points near the eastern boundary to Burns Lake.

During my stay at Atlin (60″ north), from July 1st to August 31st, 1939, *danae*, a species of late emergence in the north, did not put in an appearance until August 16th, which was subsequent to frost on the nights of August 3rd and 11th. The insects were scarce.

On my trip of 1940, I found *danae* common in the Rocky Mountains, western trench, north: McBride, July 12th, tenerals; Mount Robson, August 4th, both tenerals and mating pairs, and Tête Jaune, August 8th, with flying companions: *Sympetrum obtrusum* and *costiferum*.

Flight period: June 20th to October 10th.

Map areas, 2-14. There are two records for Alaska (Gloyd 1939).

Sympetrum decisum (Hagen)

Certainly, as to the mainland of British Columbia, this is a common species: somewhat variable as to the appearance, and very much so as to size. The face may be a creamy-brown, (in specimens not quite adult) to what the late E. B. Williamson aptly called a "cherry red." Again, as that author points out, the wings of western *decisum* may have a reddish venation, giving a distinctly tinted appearance.

My records, mainland, are: Beaver Lake, Vancouver, September 3rd-16th; Chilliwack, July 23rd, Hope district, Silver creek, July 25th-30th, Hope-Princeton trail, August 2nd, Kawakawa Lake, August 5th, Hatzic Lake, August 8th, Harrison Bay, August 9th-24th, common. These lower Fraser Valley specimens were mostly the cherry-faced form; and those of Harrison Bay district unusually large. Examples were sent to Walker, whose comment

was: "the largest specimens I have ever seen." I have also taken it: Penticton, Golden (small specimens) Kamloops (river and Lac de Jeune) and Jesmond, in the Cariboo, dates July 16th to August 29th. Walker (1927) records: Okanagan Landing, Peachland, Armstrong, Kootenay Landing, Vernon, and (1938) Cultus Lake district, Rosedale, Chaperon Lake, Liumchin Mt. Of Buckell's 26 localities, I give those best serving to extend the range: Burns Lake, 150-Mile House, Canim Lake, Prince George, Canal Flats and Osoyoos.

There is no record to date of this species on Vancouver Island. During my 1937 trip, the length of the highway, I watched for it most carefully, but with negative results.

At Atlin, B.C., 1939, (60″ north) I took my first specimen July 18th: a young male just coming into red coloration. The occasional insect was netted from that date until August 29th, but it was never plentiful. This is the most northerly record of which I have knowledge in western Canada.

On my trip of 1940, Prince Rupert to the Alberta border, I found this species emerging in numbers at Vanderhoof, July 8th, and again common at McBride, July 12th. Still more eastwardly, in the Yellowhead Pass, it was not in evidence, *Sympetrum obtrusum, costiferum* and *danae* being the species of the genus netted.

Flight period: June 15th to October 8th.

Map areas: 3-10, 13 and 14. It will be noted that it is in the seaboard areas, 1, 2, 11 and 12, for which records are lacking. It is, however, recorded from Alaska (Gloyd 1939).

Note: Harrison Bay specimens: length up to 37 mm. and wing-spread to 61 mm.

Sympetrum pallipes (Hagen)

This species, easy to identify in the field by the light stripes on the sides of the thorax, is recorded only by Walker (1927) from southern localities on Vancouver Island.

On the mainland I have records: Crawford Bay and Nelson, West Kootenay, August 17th-24th, 1928; Cultus Lake (runway near Indian Village) emerging July 8th on; Hope (Silver creek) July 26th-29th, (Kawakawa Lake) July 31st, (Texas Lake) August 3rd, flying in cop.; Harrison Bay, August 9th. At Beaver Lake, Vancouver, I have taken it to September 24th. It would appear to have a flight period of about fifteen weeks.

My records on Vancouver Island were: Sooke, emerging as early as June 6th; and at Florence Lake, still emerging, June 29th-July 4th. In the Nanaimo district: Wellington Lakes, there were adults but also tenerals, July 14th. Again, upon reaching Forbes Landing, July 25th, my notes read: "mostly tenerals seen," and, under date August 12th: "now some adults." The progressive emergence, over virtually a two months' period, would appear to be

governed by climatic conditions in the short distance northward of 200 miles. Or, of course, the species may be one of sporadic emergence, in which case the tenerals on the water might be observed rather than the adults away from it. On the "Forbidden Plateau" (3,200 feet), Courtenay district, I took a final specimen August 26th.

Further distribution: In 1938 *pallipes* was emerging at Kaslo, June 24th, and I also took it at Penticton, July 17th. Walker (1938) records: Cultus Lake district, also Rosedale and Chaperon Lake. Buckell (1938) contributes Christina Lake, Douglas Lake, Mable Lake, Moyie, Nelson, Okanagan Landing, Oliver, Osoyoos, Quilchena, Stump Lake, Vaseaux Lake and Wasa.

Flight period: June 6th to September 24th.

Map areas: 1-8.

Sympetrum obtrusum (Hagen)

In the field the white face of the *obtrusum* male serves for instant recognition from *Sympetrum decisum*, but with regard to females much more care is necessary, and, bearing upon this, the late E. B. Williamson's paper (1933) leaves nothing to be said. The morality of dragonflies is notoriously lax, a lustful male unhesitatingly seizing the female of his or another species. In a genus such as *Sympetrum*, where six or more species may be flying together, it is unwise for the collector to accept mated pairs as identification of the female. I mention the point here since (an extreme instance) I have taken an adult red *obtrusum* male holding a black *Sympetrum danae* female: a case where mistaken identity must fail as an excuse. However, fertilization apparently does not result, for the species in this genus produce nothing leading to suspicion of hybridism.

Distribution is general. I have records on the mainland from Vancouver to Harrison Bay and Hope, and again at Crawford Bay and Nelson, West Kootenay. By filling in with Walker's Okanagan records the gap is covered. On Vancouver Island my records are from Forbes Landing district only, but I had left the southerly section before this species might be expected. My notes read: "Flying: just coming into red colour," July 25th; "now almost adult," July 29th; and "full coloration," August 12th. On *Somatochlora walshii's* favoured drainage creek I recollect there was usually a well-behaved little white-faced *obtrusum*, which I permitted to stay there as a "decoy."

Walker (1927) in quoting records for *obtrusum* from Kaslo (mainland, West Kootenay) by Currie and Langford Lake and Victoria (Vancouver Island) by Osburn, appears to question correct identity. I have two specimens in my collection taken at Crawford Bay (West Kootenay), and my Forbes Landing (Vancouver Island) specimens are likewise above suspicion. The insect's range is apparently wider than believed.

Further distribution: In 1938 I took *obtrusum*, Kaslo, June 24th, emerging: Penticton, July 17th, Vernon, July 26th, Revelstoke, August 4th and Jesmond,

in the Cariboo, August 29th. Walker (1938) records: Cultus Lake district, Chilliwack and Nicola river, dates July 1st-August 30th. Buckell (1938) contributes 25 localities, from Osoyoos, on the international border, to Quesnel, July 10th, on 53″.

In 1940 I found *obtrusum* plentiful in the Yellowhead Pass area, both at Tête Jaune, August 8th, and at Mount Robson, August 4th.

Flight period: July 1st to October 19th.

Map areas: 1-10.

Leucorrhinia borealis Hagen

Walker (1927) published W. A. Newcombe's record of 1 male at Chilcotin. Since then Buckell has also taken it at Chilcotin (Big Creek), 8 specimens; and has added two new localities: Squilax, June 6th, and 100-Mile House, July 8th, both 1937. Somewhat to my surprise—for *borealis* is recorded from Alaska (Gloyd 1939)—I failed to find the species at Atlin, B.C., when collecting there in 1939.

In general appearance *Leucorrhinia borealis* is extremely like its ally, *L. hudsonica*, only larger. Length, male, 40 mm.; wing-spread 64 mm. Dorsum of abdomen with spots to segment 8, yellow in young specimens, but blood-red in aged adults. Lateral view, superior appendage, similar to its ally. *Borealis* is less widespread than *hudsonica*, but where both occur as at Red Deer, Alberta, they emerge at the same early date (about 4th week of May) and fly together until towards the end of July.

On my trip of 1940, Prince Rupert to the Alberta border, I located this species at Burns Lake, taking a male July 2nd and another July 4th. Walker (1927) refers to *borealis* as a "prairie species," and it will be noted that the above records relate to the central—more prairie-like—country. Burns Lake is the same altitude as Red Deer, Alberta, 2,700 ft.; and the trees: spruce, white poplar, willow, birch, etc. (no cedar) are identical. Waiving all question of provincial boundaries and geographical mileage, I was justified in expecting *the association of a like list of species under like environment*—and found them: *Leucorrhinia borealis* and *hudsonica*, *Cordulia shurtleffi*, *Libellula quadrimaculata*, *Somatochlora hudsonica*, *Enallagma boreale* and *cyathigerum*, and *Coenagrion resolutum*. But when comparing the odonate fauna of two fairly distant places, separated by high mountain ranges, as in this instance, certain species must be expected peculiar to each. So, to the Burns Lake, B.C., list I must include *Enallagma carunculatum* and *Tetragoneuria canis*, neither of which has been recorded from the Canadian Zone in Alberta; and to the Red Deer, Alberta, list, *Coenagrion angulatum*, that has never been found west of the Rocky Mountains. In spite of precise environmental similarity leading to a dragonfly fauna common to both, the distribution of such extraneous species still confronts us. It will be noted, of course, that these are the non-boreal species, and, south in their own range, denied migration east or west (as the case would be) by the formidable mountain ranges;

whereas the truly boreal species could work south upon either side of the mountains from an area of distribution in the northern plateau.

Flight period: records, June 6th to July 8th. This is too short for its full season which is probably, as in Alberta, from the 4th week in May to the 4th week in July.

Map areas: 5 northwardly, and 10.

LEUCORRHINIA HUDSONICA (Selys)

While this boreal species appears as early as May 14th at Vancouver (ten days earlier than the emergence at Red Deer, Alberta) and there are records showing wide distribution in British Columbia, it does not appear 'at home' southwardly in the Province: one notes the occasional specimens, but misses the swarming hordes of the insect in its truer habitat.

As Walker (1927) points out, *hudsonica* in British Columbia attains a large size, but I have taken specimens the exception to this, such as those on the "Forbidden Plateau" (3,200 feet) Courtenay district, August 26th 1937. This was my only record for the species on Vancouver Island during the months June, July, August, and including the territory Sooke to Forbes Landing: 200 miles. However, Walker gives two other localities on the Island, so it clearly occurs where conditions are suitable.

On the mainland beside Vancouver, mentioned above, I have records: Cultus Lake, June 19th, Hope district, August 2nd and Kaslo, June 14th-21st. Ricker, Lost Slough, July 1st-August 7th. Buckell contributes: lakes in the Falkland district, Aspen Grove, Bridge Lake, Chilcotin, Chase, Jesmond, Quesney, Salmon Arm and Prince George (Summit Lake).

On my trip of 1939 to Atlin (60″ north) I found this species adult upon my arrival July 6th. It occurred at the smaller muskeg pools as favoured by *Aeschna coerulea septentrionalis* and *Somatochlora septentrionalis* and not at the larger, with firm peaty edges, were *Somatochlora albicincta* and *hudsonica* were flying. *Leucorrhinia hudsonica* is an early species—quite possibly the first dragonfly to emerge at that latitude—and by July 31st the flight was about over. My last record was August 2nd, a female.

Between Prince Rupert and the Alberta border, 1940, I found this species at Smithers, June 22nd; Burns Lake, June 29th; Vanderhoof, July 8th, and Mount Robson, in the Yellowhead Pass, August 5th. At Burns Lake it was fiying with its Alberta flying mate, *Leucorrhinia borealis*.

Flight period: May 7th to August 26th.

Map areas: records, 1-5, 7, 9, 10, 11 and 13. Quite obviously this species is of wide distribution in the Province, and I see no good reason why it should not also occur in areas 6, 8 and 12. Mrs. Gloyd's Synopsis for Alaska (1939) —as might be expected—gives a number of records.

Note: I have females with a iength up to 34 mm., and a wingspread to 55 mm.

Leucorrhinia glacialis Hagen

On my Vancouver Island trip, 1937, I found this species at two localities only, and these at the far extremities of the highway south and north: Sooke, common and in cop., June 7th-9th; and Forbes Landing, breeding, July 25th to August 22nd. In the latter area it was flying with *Leucorrhinia proxima,* and, Anisoptera and Zygoptera, no less than 33 other species.

Distribution: Walker took *glacialis* at Loon Lake, Nanaimo district, Vancouver Island, July 19th 1913, and on the mainland, Prince Rupert, June 10th-July 1st. Buckell contributes: Chase, Horsefly, lakes in the Salmon Arm district, Meadow Lake, Quesnel and Prince George (Summit Lake).

On my trip of 1940, Prince Rupert to Alberta border, the only habitat I found for this species was at Terrace, June 17th, where it was common. Terrace is only a few miles east of Prince Rupert, where Walker (1927) found it to be the most numerous species of the genus: "outnumbering *L. hudsonica* at least ten times."

Flight period: June 7th to August 22nd.

Map areas: 1, 2, 5, 10 and 11.

Leucorrhinia proxima Calvert

Walker (1927) gives a number of localities for *proxima,* both on Vancouver Island and the mainland. On my Vancouver Island trip, 1937, I took specimens in the Nanaimo district on Newcastle, flying with *Sym. illotum* and *Pachydiplax longipennis,* July 16th; and at Forbes Landing, flying at several bodies of water, July 25th to August 22nd. By the latter date they were becoming scarce. *Glacialis* was also present in Forbes Landing area; a fact I mention since Walker records that he found the two species associated in the Nanaimo district, at Loon Lake, July 19th 1913.

Distribution: Atlin (E. M. Anderson), Victoria, Vancouver Island (Hagen) Vancouver, Stanley Park (E.M.W. and F.C.W.) Revelstoke (E.M.W.), Kaslo (Currie and F.C.W.) June 24th, Crawford Bay (F.C.W.) June 28th. Buckell contributes 15 localities, from Prince George (Summit Lake) in the north to Osoyoos on the international border; and Princeton and Tatla Lake in the west to Revelstoke, May 15th-August 14th.

In 1940, between Prince Rupert and the Alberta border, I took but two specimens of *proxima:* a male at Smithers, June 22nd, and an aged male at Red Pass (in the Yellowhead Pass) July 24th.

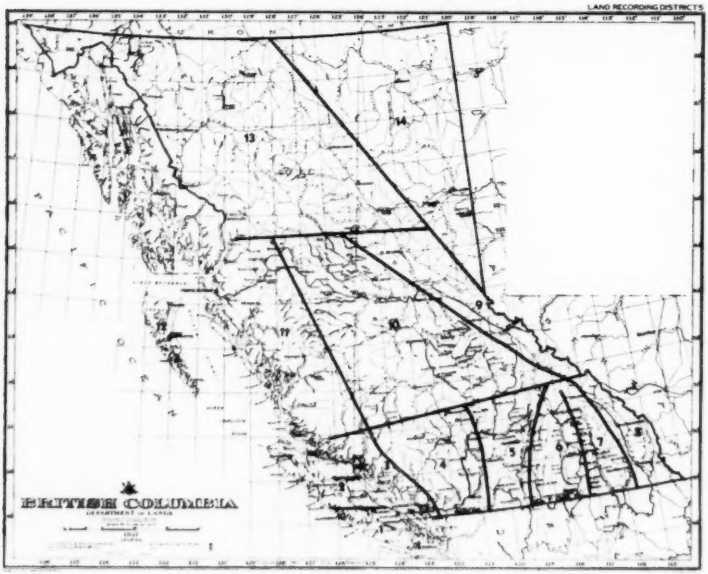
Flight period: records, May 15th to August 22nd.
Map areas: 1-7, 9, 10 and 13. Also Alaska (see Gloyd 1939).

Leucorrhinia intacta Hagen

Intacta was the commonest dragonfly at the Golf Club slough, Chilliwack, July 15th-25th 1936. Like the other species of the genus they will settle on

bushes, but seem to prefer a warm road in the blazing sun. The male, after the manner of *Libellula quadrimaculata* and *lydia*, will follow the ovipositing female, hovering some twelve inches above the water and slightly behind his mate, while she busies herself distributing eggs where the water plants touch the surface. That duty finished for the time being, (and presumably to avoid being seized again) she will shoot perpendicularly twenty or thirty feet into the air. In the number of pairs I observed, the male seemed to miss this manoeuvre, for he remained on the water, apparently searching for her. The insects in this Province are inclined to be large. Length up to 37 mm.; wing-spread up to 60 mm.

Walker (1927) gives three Vancouver Island records: Alberni, Saanich district and Elk Lake, and, on the mainland, Vernon, Okanagan district. Beside the occurrence in numbers at Chilliwack, discussed above, the insect is on the wing at Beaver Lake, Stanley Park, Vancouver, from June 13th, but



Areas of Distribution of British Columbia dragonflies.—1. Vancouver Island, south. 2. Vancouver Island, north. 3. Pacific Coast, southern. 4. West and East Cascades. 5. Okanagan Valley. 6. Monashee Range and Columbia Valley. 7. Selkirk Range and Kootenay Valley. 8. Rocky Mountain Range and its Western Trench, south. 9. Rocky Mountain Range and its Western Trench, north. 10. Central Hinterland. 11. Pacific Coast, northern. 12. Queen Charlotte Islands. 13. Northern Hinterland. 14. Eastern Foothills, Rocky Mountains. Published with the permision of the Minister of Lands, Province of British Columbia.

it is not common there. My Vancouver Island records are different from those given by Walker, I therefore state them, with their dates: Thetis Lake district: Long Lake, a female netted, others seen, June 25th; Upper Thetis Lake, common, June 26th; Florence Lake, a few seen, June 29th-July 4th; on Goldstream creek, a female, July 4th; Wellington Lakes, 2 females, July 14th. One of the last mentioned was of the sooty winged form: the first I have taken in this Province.

Further mainland records: Kaslo, emerging, June 24th, Crawford Bay, June 28th, both 1938. Buckell's localities: Chase, Salmon Arm, Westbank, Creston, Oliver and Osoyoos. J. Wynne, Enderby, June 4th.

Flight period: records, May 1st to August 16th.

Map areas: 1, 3, 4, 5 and 7.

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Taxonomic and Bionomic Notes on the Grasshopper Melanoplus impudicus Scudder (Orthoptera: Acrididae)

Ashley B. Gurney

During 1940 *Melanoplus impudicus* Scudd. was discovered to be well established on shale barrens on the western slope of the Massanutten Mountains a few miles from Woodstock, Va. These mountains rise from the floor of the Shenandoah Valley, between the Blue Ridge to the east and the Alleghenies and other mountains of the Appalachian system to the west. On the slopes of the Massanutten Range are many areas of very fine talus, resulting from the weathering, on the steep hillside, of protruding layers of shale. These areas, very small to many acres in extent, are called shale barrens and support a distinctive flora and, at least in part, a distinctive fauna. There are no published Virginia records of *M. impudicus*, though it was first taken in the State by Morgan Hebard at Hot Springs in 1916. Comparatively little has been published concerning the species, and since it is such a characteristic member of the insect fauna of the shale barrens all available information on variation, taxonomy, distribution, and habitat preferences has been brought together for presentation here. While there is some diversity in the habitats occupied by this grasshopper, it is a good example of a widely distributed species that is abundant only in localized areas which serve as favorable ecological niches.

Workers to whom I am indebted for a generous response to my requests for cooperation regarding field notes and specimens include R. H. Beamer of the University of Kansas, Irving Cantrall of the University of Michigan, B .B. Fulton of the North Carolina State College, C. E. Mickel of the University of Minnesota, and E. S. Thomas of the Ohio State Museum. At the Academy of Natural Sciences of Philadelphia, Morgan Hebard and J. A. G. Rehn placed their collections and field notes at my disposal during a visit there. It was my privilege to examine the collection of W. T. Davis at the Staten Island Institute of Arts and Sciences, and, during a visit to Cambridge, Mass., Nathan Banks permitted me to examine the types of *impudicus* and the material collected by A. P. Morse contained in the Scudder Collection. T. H. Hubbell of the Universities of Florida and Michigan generously furnished detailed field notes on specimens from numerous localities, and J. J. Friauf kindly allowed me to use data on specimens collected in connection with a doctorate thesis. Harry A. Allard of the Bureau of Plant Industry, U. S. Department of Agriculture, in whose company many collecting trips have been made, first showed me the shale barrens. He intends to publish an account of the flora of the shale barrens and has helped with the botanical notes presented here.

Melanoplus impudicus (Fig. 1) is a medium-sized, long-winged species. Sixteen representative specimens selected from the series examined have the following minimum and maximum measurements in millimeters: Length of body ♂ 16, 20.5; ♀ 22, 27; of pronotum, ♂ 4, 5; ♀ 5, 6.5; of tegmen, ♂ 11, 17; ♀ 14.7, 21.5; of hind femur, ♂ 10, 12.5; ♀ 12, 16. The measurements given by Blatchley (1920, p. 418) show less variation, presumably because they were based mainly if not entirely on his Indiana series. Specimens from Florida average larger than those from New Jersey. The tegmina fail by 2 mm. to reach the tips of the hind femora in some specimens, and in a few exceed them by as much as 3 mm. The tegmina average longer in specimens from Georgia, Florida, and other southeastern States than in specimens from more northern localities, but those of a male from Chattanooga, Tenn., are among the shortest of any examined. Dr. Hubbell writes that the majority of his Oklahoma specimens are comparatively robust and have the tegmina about as long as the abdomen (♂) or slightly shorter (♀), but that certain specimens have the tegmina distinctly surpassing the abdomen in males and slightly so in females. None of his Oklahoma specimens is said to be as elongate and long-winged, however, as the average of Florida series, nor is any especially short-winged.

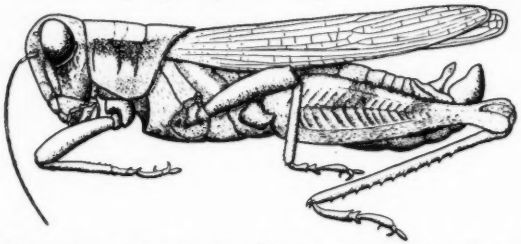

Fig. 1. *Melanoplus impudicus* Scudder. Habitus, ♂, lateral view. Pughs Run, Shenandoah County, Va., September 2, 1940.

The general coloration of *impudicus* is dull in most specimens, but the pale, diagonal, episternal stripe is usually conspicuous. The most noticeable variation is that some specimens, especially those from North Carolina and other southeastern States, are more contrastingly colored, much of the ground color being ochraceous. The femoral bars vary from nearly lacking to conspicuous, and the dark horizontal bar on the lateral lobe of the pronotum may be shining black, particularly in males, or poorly developed. Examples from the shale barrens in Virginia are noticeably darker and more slate colored on the average than those from pine barrens in New Jersey.

Melanoplus impudicus was described by Scudder (1897)[1] from one male and two females, and Rehn and Hebard (1912, p. 81) designated the male

[1] The name *impudicus* actually dates from a key to the species of *Melanoplus* (Proc. Amer. Philos. Soc. **36**(154):5-35, 1897) issued by Scudder preliminary to the revision of the Melanopli which appeared later the same year.

as lectotype. The latter has the tegmina extending 1 mm. behind the apices of hind femora, and the dark bars of the hind femora rather conspicuous. The label data are "Geo. S. H. Scudder Coll. *Mel. impudicus*. Scudder's type, 1895. Type 735." One female has the data, "Geo. Morrison. S. Henshaw. *Mel. impudicus*. Scudder's type, 1895. Type 735." Morrison is in extreme northeastern Georgia near Iuka. The tegmina of this specimen extend about 3 mm. beyond the hind femora and the colors are rather conspicuous, as in other southeastern material of *impudicus*. The second female, a somewhat distorted specimen originally collected in alcohol, is from Monticello, Miss.

As in most species of *Melanoplus*, the most useful structures for specific recognition and for determining the closest relatives are the male terminalia. Since *impudicus* has no very close relatives, it is usually possible to identify it by the shape of the cercus (Fig. 5); the furcula and supraanal plate are also useful. The subapical depression of the cercus and the subapical angle of the ventral margin of the same organ are somewhat variable, but not to an extent that is confusing. Even more distinctive than the external terminalia is the aedeagus, here illustrated in lateral and dorso-posterior views (Figs. 15, 20). The epiphallus is shown in lateral view (Fig. 4), but, like the aedeagus, it seldom need be examined for the recognition of this species, though in certain sections of the genus *Melanoplus* both aedeagus and epiphallus are most important. In the illustration of the apex of the abdomen of *M. tuberculatus* Morse (Fig. 13), a species related to *impudicus*, the cavity which contains the epiphallus and aedeagus is indicated. Discussions of the dissection, study, and preservation of the aedeagus and epiphallus are given by Hubbell (1932, pp. 6-11) and Gurney (1940, pp. 100-103).[2]

The nearest relatives of *impudicus* are *Melanoplus fasciatus* (F. Walk.) and *M. frigidus* (Boh.). Less closely related is *M. tuberculatus*. To assist in the recognition of these species, the cercus, furcula, supraanal plate, and aedeagus of each have been illustrated, and those of *M. keeleri luridus* (Dodge), a species associated with *impudicus* on the Massanutten shale barrens, have also been included. A lateral view of the epiphallus has been shown in the case of *impudicus* and *fasciatus* (Figs. 4, 11).

M. impudicus is known to occur in 17 States, from Long Island to Florida and west to Illinois and Oklahoma (Fig. 2). The most important distributional references are those of Blatchley (1920), Davis (1928), Fox (1928), Hebard (1931, 1934), McNeill (1899), Morse (1904, 1907), Smith (1910), Rehn (1904), and Rehn and Hebard (1916). E. S. Thomas writes (in litt., October 21, 1940) that he has not found *impudicus* in Ohio. In view of Mr. Thomas' careful collecting in Ohio, the species probably does not occur there, unless in a restricted area that has escaped his attention, which, in view of its specialized habitat, is possible.

Rather complete habitat notes are available for several regions in which

2 An important paper, entitled "A comparative study of the subfamilies of the Acrididae (Orthoptera) primarily on the basis of their phallic structures," has recently been published by H. Radclyffe Roberts (Proc. Acad. Nat. Sci. Phila., **93**:201-246, ill., 1941.

impudicus occurs, and comparison shows that throughout its range the preference for a dry, rather open situation is marked, many of the plant associations being similar. The pine barrens of New Jersey, of which *impudicus* has frequently been cited as a characteristic species, have been discussed by Stone (1908, 1911) and Fox (1914, 1928). The Penniquid barrens of Long Island are rather similar. In their study of the sand areas of Illinois, Hart and Gleason (1907) recorded *impudicus* from the blowout association of the sand hills and the black jack association of the bluffs, and several plants given as conspicuous members of the latter association likewise are typical of the barrens of Virginia. Naturally many species differ, as in the case of western elements that enter Illinois, but the close similarity of genera is well marked. The bluff habitat described for Illinois is probably similar to the Gibson County,

Fig. 2. Distribution of *Melanoplus impudicus* Scudder.

● Localities from which one or more specimens have been examined by the author.

○ Localities, based on published records, from which no specimens have been examined.

△ Localities based on previously unpublished data furnished by T. H. Hubbell.

PLATE I

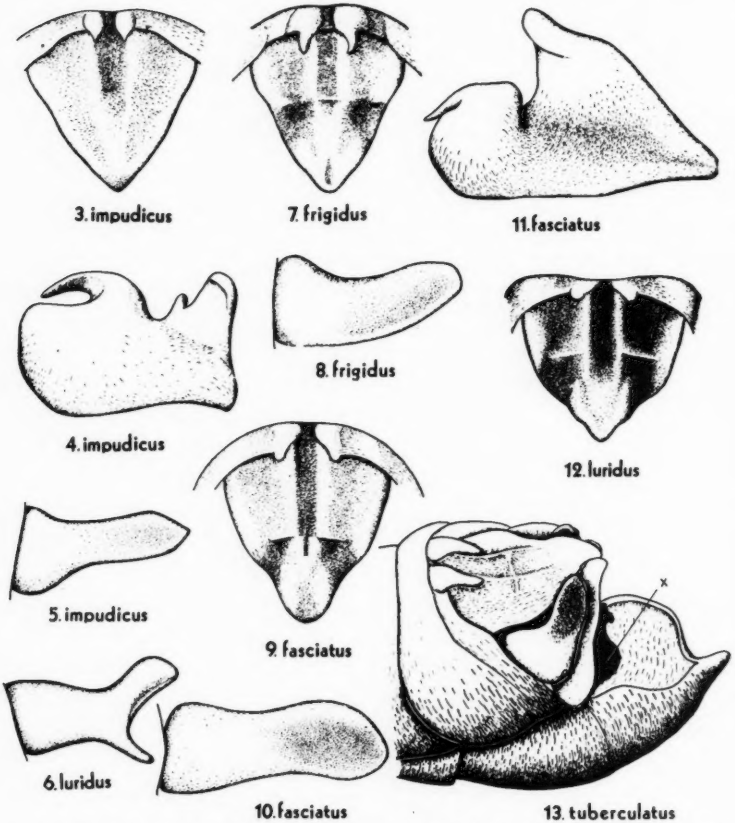

Fig 3. *M. impudicus*. Furcula and supraanal plate, dorsal view. Shale barrens just north of Pughs Run, Shenandoah County, Va., September 22, 1940.—Fig. 4. Same. Lateral view of epiphallus from left side. Pughs Run, Shenandoah County, Va., September 2, 1940.—Fig 5. Same. Left cercus. Same specimen as in Fig. 3.—Fig. 6. *M. keeleri luridus* (Dodge). Left cercus Ansonia, Conn., October 5, 1901.—Fig. 7. *M. frigidus* (Boheman). Furcula and supraanal plate, dorsal view. Pallastunturi, Finland, September, 1938.—Fig. 8. Same. Left cercus. Same specimen as in Fig. 7.—Fig. 9. *M. fasciatus* (F Walk.) Furcula and supraanal plate, dorsal view. Cummington, Mass., 1200 ft., July 29, 1934.—Fig. 10. Same. Left cercus. Same specimen as in Fig. 9.—Fig. 11. Same. Lateral view of epiphallus from left side Same specimenas in Fig. 9.—Fig. 12. *M. keeleri luridus*. Furcula and supraanal plate, dorsal view. Same specimen as in Fig. 6.—Fig. 13. *M. tuberculatus* Morse. Dorso-lateral view of apex of abdomen. Comanche County, Okla., August 5, 1938. X, cavity from which aedeagus and epiphallus have been removed for study. All figures based on males. (Drawings by the author.)

PLATE 2

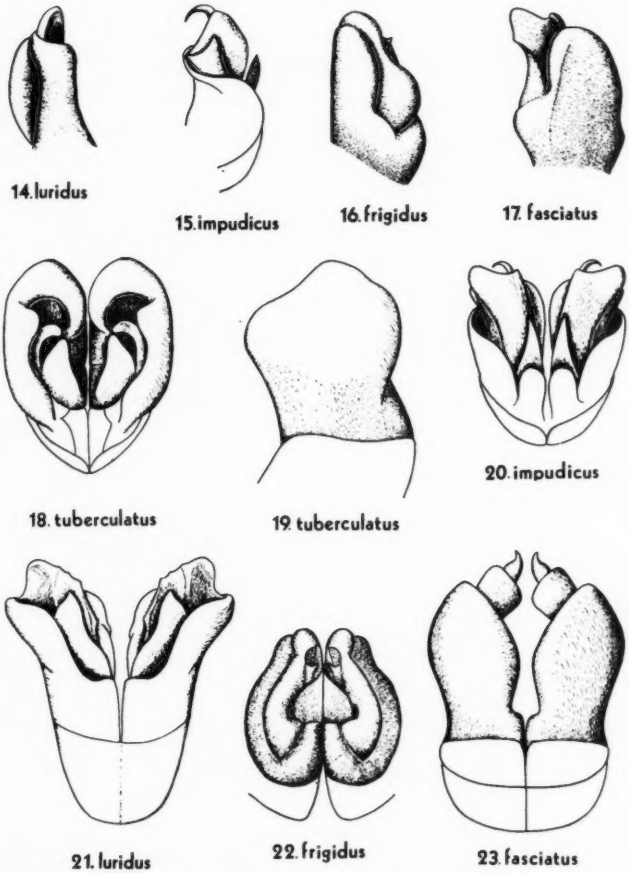

Fig. 14. *M. kecleri luridus*. Lateral view of aedeagus from left side. Pughs Run, Shenandoah County, Va., September 2, 1940.—Fig. 15. *M. impudicus*. Same view. Same specimen as in Fig. 4.—Fig. 16. *M. frigidus*. Same view. Same specimen as in Fig. 7.—Fig. 17. *M. fasciatus* Same view. Same specimen as in Fig. 9.—Fig. 18. *M. tuberculatus*. Dorso-posterior view of aedeagus. Same specimen as in Fig. 13.—Fig. 19. Same. Lateral view of aedeagus from left side. Same specimen as in Fig. 13.—Fig. 20. *M. impudicus*. Dorso-posterior view of aedeagus. Same specimen as in Fig. 4.—Fig. 21. *M. kecleri luridus*. Posterior view of aedeagus. Same specimen as in Fig. 14.—Fig. 22. *M. frigidus*. Dorso-posterior view of aedeagus. Same specimen as in Fig. 7.—Fig. 23. *M. fasciatus*. Same view. Same specimen as in Fig. 9. All figures based on males. (Drawings by the author.)

Ind., locality where Blatchley (1920) found *impudicus* along the terrace of the Wabash River. In Oklahoma *impudicus* has been taken in 3 of the 11 biotic districts of the State as outlined by Blair and Hubbell (1938), and these authors indicate its probable occurrence in a fourth, the Ozark district. They record the species from the Ouachita, Cherokee Prairie, and Osage Savanna districts. The plant associations, rocky hillsides of thin soil, and ridges topped by escarpments which characterize these districts remind one of other habitats in which this grasshopper occurs.

Fig. 24 shows a large bare area at Pughs Run, a few miles east of Woodstock, Va., and Fig. 25 is of an open spot and surrounding vegetation at Short Mountain, about 15 miles farther south. The chestnut oak (*Quercus montana* Willd.) is dominant, with black jack or barren oak (*Q. marilandica* Muench.), Virginia scrub pine, and pitch pine occasional. The low blueberry (*Vaccinium vacillans* Kalm.), the snakeroot (*Liatris scariosa* Willd.), the wild pea (*Tephrosia virginiana* (L.) Pers.), the asters *Aster oblongifolius* Nutt. and *A. laevis* L., and the butterfly pea (*Clitoria mariana* L.) are characteristic members of the shale-barren flora. The day-flower (*Commelina erecta* L.), of the spiderwort family, is frequent where a foothold may be secured, and the red cedar also is present. Scarcely any grasses occur where we found the grasshopper, and the bare weathered shale, gradually drifting downward and with knife-like exposed layers often protruding, frequently extends to the edge of the shrub and tree zone. In other places there are some grasses and sedges. Mr. Allard finds that this flora shows certain affinities with that of the coastal plain, as exemplified by the milk pea (*Galactia regularis* (L.)) and the mint *Trichostema lineare* Walt.

That the specimen here recorded from Hot Springs, Va., was found in a habitat similar to the Massanutten area described above is indicated by Hebard's field notes, "In pitch pine, oaks and oak scrub, . . . on steep upper slopes of shaly hill."

In the dry portions of the New Jersey pine barrens characteristic plants such as black jack and chestnut oaks, pitch pine, sassafras, the low blueberry, and the goldenrod (*Solidago erecta* Pursh.) agree with the Massanutten flora. Habitat notes associated with specimens of *impudicus* in the Philadelphia collections include mention of gravelly uplands, openings among pines with sweet fern, oak, and huckleberry scrub, and sparse grass. Very similar is the habitat in the Pocomoke State Forest, Md., where J. A. G. Rehn and J. W. H. Rehn found *impudicus*, "In open woods of pine, oak, and sassafras, with ground cover of oak scrub, fox grape, and huckleberries." The barrens of Long Island described by Davis (1921) are in an area of abandoned farms where the soil is sandy and where bear-berry, junipers, red cedars, oaks, and pitch pine exemplify the relapse into forest conditions.

Similarity between the plants of the Massanutten shale barrens and the Illinois bluff black jack association is shown by the forked chickweed (*Anychia canadensis* (L.) Wood), the flowering spurge (*Euphorbia corollata* L.), the sumach *Rhus canadensis* Marsh. (*aromatica* Ait. of Hart and Gleason's list,

PLATE 3

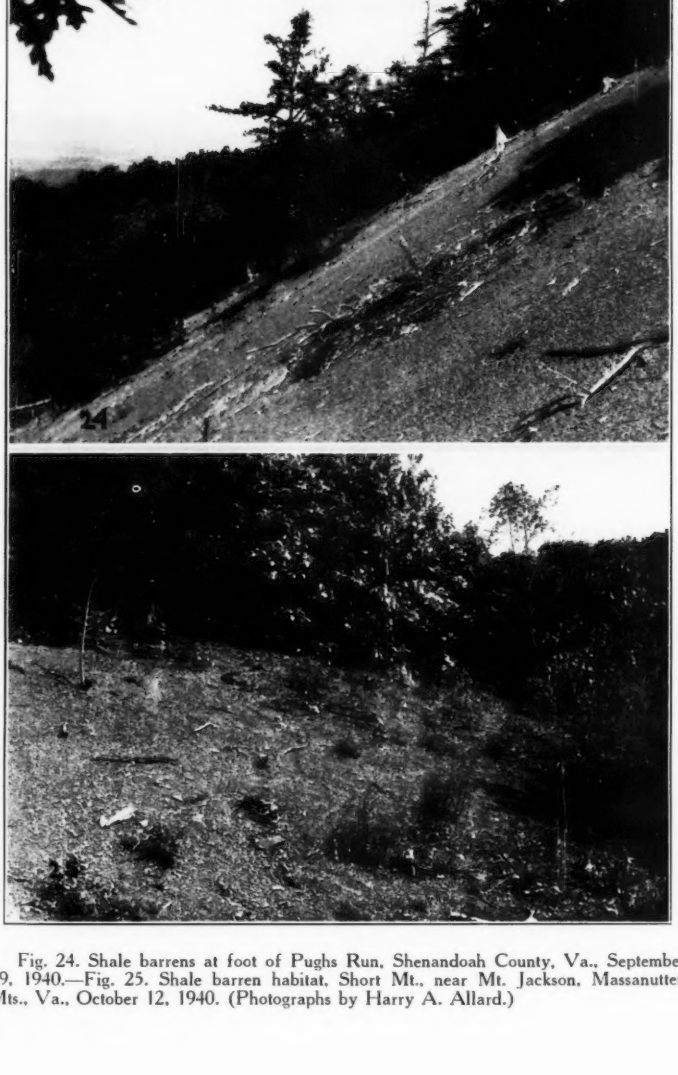

Fig. 24. Shale barrens at foot of Pughs Run, Shenandoah County, Va., September 29, 1940.—Fig. 25. Shale barren habitat, Short Mt., near Mt. Jackson, Massanutten Mts., Va., October 12, 1940. (Photographs by Harry A. Allard.)

a synonym according to Gray's Manual), and the sensitive plant (*Cassia nictitans* L.). Notes made by Blair and Hubbell show that in Oklahoma *impudicus* nearly always occurs in black jack oak or oak-hickory associations. The usual environment includes considerable second-growth oak and hickory in fairly open stands, grassy openings, sandstone outcrops, and a rather dry general condition, often along the summit of a ridge.

Field notes made by Hebard and Rehn during their extensive collecting in the Southeastern States, by Fulton in North Carolina, by Hubbell in Tennessee and Florida, and by Friauf in Florida further confirm the preference that *impudicus* shows for open woodland or wasteland habitats, often on bare soil. In Alachua, Liberty, and Walton Counties, Fla., *impudicus* has been taken in the environment known as "high pine-turkey oak" and which has been described by Hubbell and Goff (1940). Typically the dominant trees are long-leaf pine, slash pine, and the oaks *Quercus laevis* Walt. and *Q. cinerea* Michx.; the oaks frequently appear as a scrubby understory. Wire grasses (*Aristida* spp., *Sporobolus* spp.), dwarf chinquapin (*Castanea alnifolia* Nutt.), and various herbs are present. The trees are often scattered, with patchy undergrowth and much bare soil exposed. The chief soil type of this area is known as Norfolk sand. The most southeastern records for *impudicus* are those at Welaka, Fla., where Friauf took it in the above habitat on a gently rolling sand ridge. Some specimens from Florida have been collected in openings where clumps of palmetto occurred, and a few in open fields on sandy hillsides.

From the foregoing data it is apparent that *impudicus* is a grasshopper that prefers dry soil conditions and is to be found most frequently on wastelands or on bluffs or hillsides where a combination of the dryness and exposed areas, if in woodland, is available. The preferred food plants of *impudicus* are not known. While active on bare soil, this grasshopper retreats to shrubbery for concealment and probably for feeding. In view of the scarcity of grasses in certain areas where we found *impudicus* in Virginia, plants other than grasses may be included in the diet. Ball (1936) and others have demonstrated that many grasshoppers are far from being general feeders, and *impudicus* may eventually be shown to have specialized food habits.

In the northern part of its geographical range, adults of *impudicus* are most abundant during midsummer and early fall, early records being June 9 at Vineland, N. J., July 10 in Gibson County, Ind., and June 27 (recorded by Hebard, 1934, p. 196) at Alto Pass, Ill. October 12 at Pughs Run, Va., and October 8 at Atsion, N. J., are late records. Farther south adults are found over a long period and may represent more than one generation, limital records being May 27 at Raleigh, N. C., April 22 at Gainesville, Fla., and October 15 at Welaka, Fla. Fox (1928) says that in New Jersey adults are rare after September 1. He reports wintering in the egg stage, also that nymphs occurred at Vineland May 13 and during early summer.

Summary

Melanoplus impudicus, which is known from 17 States, is discussed with special reference to its recent discovery on shale barrens in the Massanutten Mountains, Va. This habitat is described and compared with others in which *impudicus* has been collected. A summary of the distribution of this grasshopper is given, and the important features of the male terminalia of this and several allied species are illustrated.

Distribution of Melanoplus impudicus Scudder

Specimens examined: 386 (210♂, 176♀), located as follows: Philadelphia collections, 206; Museum of Comparative Zoology, 52; U. S. National Museum, 42; University of Michigan, 39; W. T. Davis Collection, 31; North Carolina State College, 7; University of Kansas, 7; University of Minnesota, 2.

Localities from which *impudicus* has previously been recorded are merely listed. Records preceded by a single asterisk have been supplied by T. H. Hubbell and apply to material which I have not examined. Localities from which specimens have previously been recorded, but from which none has been examined, are preceded by a double asterisk and are followed by author citation. Specimens here recorded are in the Philadelphia collections except where otherwise noted. The initials TH indicate that T. H. Hubbell was the collector, and UM refers to the University of Michigan.

New York: Coram, Selden, Deep Pond, Long Pond (all Long Island).

New Jersey: White Horse, between Harris and White Horse, Cassville, Whitesville, Lakehurst, Stafford's Forge, New Lisbon, Atsion, Vineland, Manumuskin, Quaker Bridge, ** Jamesburg (Smith, 1910), **East Plain (Smith, 1910), **Berlin (Hebard, 1938).—Upper Plains, Ocean County, August 6, 1925, Fox, 1 ♀.—Whitings, August 15, 1920, 7 ♂, 3 ♀.—Whitesbog, August 24, 1923; Fox, 1 ♂.— Chatsworth, August 9, 1919, 2 ♂, 1 ♀; August 20, 1912, Davis, 1 ♂, 1 ♀ (Davis Coll.)—Barnegat, July 23, 1915, Hebard, 5 ♂, 1 ♀.— Near Brookville, July 1900, 2 ♂ (Davis Coll).—Parkdale, July 30, 1911, R. & H., 11 ♂, 9 ♀; 1 ♂ (Minn.); July 31, 1911, Caudell, 2 ♂, 1 ♀ (U.S.N.M.)— Batsto, July 19, 1915, Hebard, 3 ♂, 3 ♀.— Along Batsto River, Hampton Furnace to Batsto, June 30, 1912, Long, 1 ♂, 4 ♀.

Maryland: Pocomoke State Forest, 5 mi. s.w. Snow Hill, Worcester County, July 16, 1938, R. & R., 1 ♂.

Virginia: Shale Barrens just north of Pughs Run, Shenandoah County, September 22, 1940, Allard, 2 ♂ (U.S.N.M.)—Pughs Run, Shenandoah County, about 1400 ft., August 14, 1940, Gurney, 1 ♂ (U.S.N.M.); September 2, 1940, Allard & Gurney, 11 ♂, 11 ♀ (U.S.N.M.)—Short Mt., near Mt. Jackson, Massanutten Mts., about 2,000 ft., October 10-12, A. & G., 4 ♂ (U.S.N.M.)— Hot Springs, 2,000 ft., July 6, 1916, Hebard, 1 ♂.

North Carolina: Raleigh, May 27, 1936, 1 ♂ (N.C.)— Spout Springs, June 6, 1929, Fulton, 1 ♂ 2 ♀ (N.C.); 3 ♂ 1 ♀ (U.S.N.M.)—Southern Pines, July 9, 1915, Manee, 1 ♀.—Hoffman, July 4, 1928, 2 ♂, 1 ♀ (N.C.)—Murphy.

South Carolina: Spartanburg, Columbia, Denmark.

Georgia: Morrison, Currahee Mt., Dalton, Sand Mt., Chickamauga, Warm Springs, Spring Creek, **Blue Ridge (Morse, 1904), **Lost Mt. (R. & H., 1916).—Groveland, September 21, 1917, R. & H., 2 ♀.—Vidalia, June 11, 1922, 2 ♂, 1 ♀.—Tallulah Falls, July 18-19, 1924, Fox, 10 ♂, 6 ♀, 1 juv. ♀.—Toccoa, June 20, 1924, Fox, 2 ♂, 1 ♀.—Locust Grove, June 10, 1924, Fox, 1 ♀.—*Augusta, May 8, 1937, TH, 1 ♂.

Florida: Gainesville, April 22, 1929, TH, 2 ♂, 5 ♀ (UM); May 15, 1936, TH, 4 ♂, 1 ♀ (UM); *May 4, 1936, TH, 6 ♂, 1 ♀, 2 last instar juv. ♀.—*Welaka, Putnam County (Univ. Fla. Conservation Reserve, all Friauf, 1940), June 5, 1 ♀; July 13, 3 ♂; July 15, 1 ♀; October 15, 1 ♀.—Alachua County, near Newberry, May 23, 1936, TH, 2 ♂, 1 ♀ (UM).—Woodville, September 1, 1915, R. & H., 1 ♂, 5 ♀.—Apalachicola River Valley, at Chattahoochee, Gadsden County, July 28, 1925, TH, 1 ♀ (UM).—"Camp Torreya," Liberty County (all TH, 1925), July 29, 2 ♀ (UM); July 30, 1 ♂, 1 ♀ (UM); July 25, 1 ♂ 5 ♀ (UM); *July 28, 1 ♂.—Rock Bluff Landing, Liberty County, July 24, 1925, TH, 1 ♂, 1 ♀ (UM).—Carrabelle, September 2-3, 1915, R. & H., 1 ♂, 5 ♀.— Franklin County, 7 mi. n.e. Lanark, July 20, 1938, Hubbell & Friauf, 1 ♂ (UM).—DeFuniak Springs, June 5, 1924, TH, 1 ♂ (UM).—Pensacola, July 12, 1934, J. D. Beamer, 1 ♀.

Tennessee: Chattanooga, July 5, 1922, TH, 1 ♂ (UM).—Lookout Mt. (near Chattanooga).

Alabama: Lookout Mt. (near Valley Head), Cheaha Mt. (near Anniston).—Camp McClellan, Choccolocco Mt., Calhoun County, July 13, 1925, H. D. Smith, 2 ♂, 3 ♀ (UM).—Dothan, September 6-7, 1915, R. & H., 1 ♀.

Mississippi: Meridian, Monticello.

Indiana: Gibson County.

Illinois: Forest City, Bath, Williams Mt., **Havana (Hart & Gelason, 1907), **Alto Pass (Hebard, 1934), **Dixon Springs (Hebard, 1934).—Prospect Hill, Herod, Cache.

Missouri: *Pulaski County, July 25, 1926, Hubbell, 1 ♂, 1 ♀.

Arkansas: Eagleton, Mena, **Madison, Boone, Carroll, Newton, Marion, and Washington Counties (McNeill, 1899), ** Blue Mt. Sta. (Morse, 1907).—Rich Mt. Sta., August 2, 1905, Morse, 1 ♀ (M. C. Z.)

Kansas: Cherokee County, Chautauqua County.

Oklahoma: Caddo, Howe.— *Delaware County, near Rose, Mayes County, June 20, 1938, W. F. Blair, 2 ♂, 3 ♀.—*Mayes County, near Salina, June 28, 1938, Blair, 5 ♂, 8♀.—*Rogers County, near Catala, July 24, 1926, TH, 1 ♂.—*Osage County, near Turley, June 28, 1937, Blair, 5 ♀.—*Adair County, near Stilwell, June 19, 1938, Blair, 2 ♂, 11 ♀.—*LeFlore County, near Poteau, June 18, 1938, Blair, 1 ♂.

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Geographic Variation in Garter Snakes of the Species Thamnophis sirtalis in the Pacific Coast Region of North America

Henry S. Fitch

Introduction

Investigation of the western forms of garter snakes of the species *Thamnophis sirtalis* was begun after the completion of an extensive systematic study (Fitch, 1940) of the *Thamnophis ordinoides* group in the same area. The *ordinoides* complex is represented by eleven forms, which show a remarkable degree of divergence in different directions, not only in structural characters, but in habits and habitats as well.

Within the *ordinoides* complex the principle of adaptive radiation as defined by the late W. D. Matthew is splendidly illustrated. Study of the *sirtalis* group was undertaken with the idea of comparing its evolutionary responses in diverse environments with the responses of the *ordinoides* complex under the same diverse influences. As compared with *ordinoides*, *sirtalis* is notably stable in its characters. Van Denburgh and Slevin (1918) published hundreds of individual scale counts of the specimens examined by them. These counts show that the numbers of body scale rows, supralabials, infralabials, and preoculars are constant in *sirtalis* throughout the western states, whereas in *ordinoides* in the same region all these characters are highly variable. The only scale characters which showed marked geographic variation were numbers of gastrosteges and numbers of urosteges (see Figs. 1 and 2). Apparently these two characters furnished the main basis for the taxonomic treatment accorded *sirtalis* by Van Denburgh and Slevin. They recognized three forms in the western United States: *parietalis* of the Great Plains and Rocky Mountains region, *concinnus* of British Columbia, Washington, western Oregon, and northwestern California, and *infernalis* of the remainder of California, western Nevada, and the Klamath Lakes region of Oregon.

In view of the stability in most scale characters, the relatively slight degree of geographic differentiation in numbers of gastrosteges and urosteges, and the high degree of individual variability in these latter characters, as shown by Van Denburgh's and Slevin's material, it is not profitable to make a further investigation of scale characters in *sirtalis*. The scale counts already available, though inadequate to show the exact amount of difference between local populations, suffice to show the general trends of scalation throughout the group, the range of individual variation within populations, and the approximate average differences between populations.

The differences in counts of gastrosteges and urosteges in the opinion of

the writer do not in themselves warrant subspecific divisions, though, of course, they are deserving of consideration, along with other variable characters, in arbitrarily setting up subspecific boundaries between the various populations. In all instances where substantial series are available, overlapping in gastrostege and urostege counts between populations of the supposed subspecies can be shown.

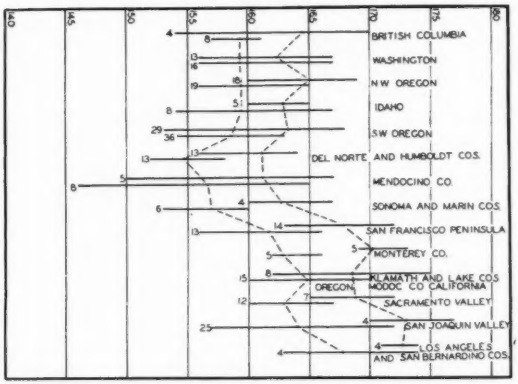

Fig. 1. Diagram showing geographic variation in numbers of gastrosteges in populations of *Thamnophis sirtalis* (based upon scale counts published by Van Denburgh and Slevin, 1918, pp. 195-198 and 201-202). Broken line at right connects means in series of males; broken line at left connects means in series of females. Note that differences are slight between populations, with much overlapping in most instances, and that in general there are continuous trends toward reduction in numbers from south to north, and from the interior to the coastal region.

The variation in numbers of gastrosteges and urosteges among the western races of *Thamnophis sirtalis* is no greater than that within the single subspecies *Thamnophis ordinoides vagrans*. The rather abrupt increase in number of gastrosteges in the *sirtalis* population of the San Francisco Peninsula as compared with the population north of San Francisco Bay in Marin and Sonoma counties does not justify separating these populations subspecifically in view of the fact that both have the same peculiar color pattern. Within the subspecies *Thamnophis ordinoides atratus* there is just as much difference in gastrostege numbers between the population of the San Francisco Peninsula and that of the east side of San Francisco Bay, and there are also accompanying differences in color pattern between these *atratus* populations.

As far as scale characters are concerned, then, all *sirtalis* from the Pacific Coast region might be assigned to the same subspecies. Investigation of color pattern characters has indicated that in them differentiation has proceeded further, and that throughout geographic populations they are rather constant, distinguishing all or most individuals from the individuals of other geographic populations. These differences are considered sufficient, in some instances, to justify making subspecific divisions, and the races herein recognized are based

mainly on characters of color and pattern. The areas in which the principal geographic changes in color pattern take place often do not coincide with those in which the most marked changes in numbers of gastrosteges and urosteges occur. Hence the arrangement presented here differs greatly (both in number of forms recognized, and range limits) from the generally accepted classification of Van Denburgh and Slevin (1918) which was seemingly based almost entirely on numbers of gastrosteges and urosteges.

My conception of the various forms is to a large extent based upon field observations on living snakes throughout much of the area considered in this paper. The snakes have a pattern of contrasting colors, which are brilliant in life, but which become obscured in preserved material as the color fades. Even though the actual colors are much dulled, the pattern can usually still be discerned. Many specimens have been so darkened and stained by preservation in strong formalin that even the pattern is obscured. Much of the preserved material available is therefore of little or no value for a study of color characters. This fact, however, does not justify the disregarding of color characters. To represent relationships accurately, any system of classification must take into consideration all available characters.

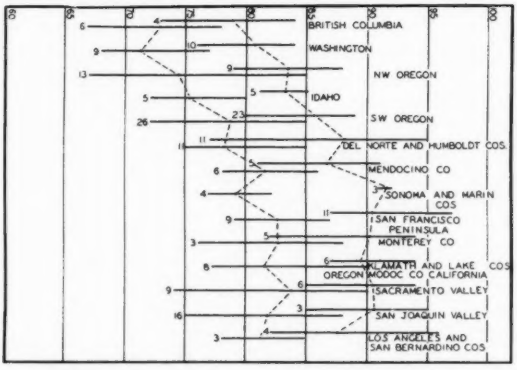

Fig. 2. Diagram showing geographic variation in numbers of urosteges in the same populations of *Thamnophis sirtalis* represented by figure 1. Note that trends in numbers of urosteges in general parallel trends in numbers of gastrosteges.

Van Denburgh and Slevin discussed variation in coloration only briefly in their revision. After mentioning the fact that San Joaquin Valley specimens usually can be readily distinguished from those of the San Francisco Peninsula (though both populations were included in their subspecies *infernalis*), they state:

> The differences are too intangible to describe, but they must exist and may become more evident when larger series can be studied. Some of the color differences which we now regard as individual may prove to be geographical, and the day may come when

the herpetologist, with enormous series, will emulate the ornithologist and the mammalogist in multiplication of subspecies.

Under the discussion of their composite subspecies *concinnus* (including representative populations of all four subspecies recognized in this paper) the same authors stated (*op. cit.*: 198):

> While a dark style of coloration with a tendency toward narrow lines is characteristic of this subspecies, this type of coloration is by no means constant. Specimens similar in color to the type of *pickeringii* seem to be very rare even in the far north. In general, the differences from *T. s. parietalis* and *T. s. infernalis* seem to lie in an increase in the dark pigment, both dorsally and ventrally, rather than in marked narrowing of the lines, or a reduction in the amount of red in the coloration. Some specimens from Oregon are no darker than Californian *T. s. infernalis*, and show red heads and often much red on the body. Others are quite dark. Upon the whole, and notwithstanding wide individual variation everywhere, it may be said that coloration becomes lighter toward the south and is gradually changed to that of *T. s. infernalis*. This color change seems to occur more rapidly (i. e., farther north) than the change in number of gastrosteges.

Color descriptions are here included for specimens considered typical of each of the four subspecies. Color terms employed are those of Ridgway (1912). The specimens used had all been preserved in alcohol for periods of months or years, and their colors were much faded as compared with those of living individuals. However, the descriptions given should be comparable to those in other preserved specimens.

In my study of the *Thamnophis ordinoides* complex, special effort was made to collect data bearing on the habits of the various forms. For the present study no such detailed data were available in quantity, so possible adaptational significance of observed structural differentiation is not apparent. However, it seems evident that *sirtalis*, as compared with *ordinoides*, is notably constant throughout its range as regards preferred habitat, methods of foraging, and food sources utilized, and that individuals of *sirtalis* are more adaptable and versatile in their behavior than are individuals of *ordinoides*. They utilize a wider range of food sources, are less restricted to a narrow ecologic niche, and occur through a wider range of habitat conditions.

In the course of this study, I have examined 62 specimens of the subspecies *pickeringii*, 57 *concinnus*, 352 *tetrataenia*, and 122 *infernalis*. These include the specimens examined and listed by Van Denburgh and Slevin (1918) in the California Academy of Sciences, Leland Stanford Junior University Natural History Museum, and Museum of Vertebrate Zoology, University of California, and new material not seen by these authors.

For facilities provided for this study at the Museum of Vertebrate Zoology, I am indebted to the late Dr. Joseph Grinnell and to Dr. Jean M. Linsdale and Mr. Thomas L. Rodgers. Mr. Joseph R. Slevin of the California Academy of Sciences and Dr. Albert W. Herre of the Stanford Museum of Natural History have kindly permitted examination of the garter snakes in the collections under their care. Dr. Leonhard Stejneger of the United States National Museum has very kindly examined type material in the National Museum on my behalf, and has furnished important information regarding it. Assistance

rendered by the Work Projects Administration, O. P. 65-1-08-113, Unit C-1, is acknowledged.

Specific Characters

Thamnophis sirtalis is of moderate size, usually between two and three feet in total length in adults. Size probably is subject to geographic variation; in some areas these snakes attain consistently larger size than they do elsewhere. Adult females are markedly larger than males in average and maximum size.

In most scale characters the species is remarkably constant over its extensive range. On top of the head the plates consist of the rostral, the paired internasals, the paired prefrontals, the frontal, with a supraocular on either side, and the large paired parietals; except for rare abnormalities none of these scales varies perceptibly in size, in shape, or in position relative to adjacent scales. On each side of the head are the anterior and posterior nasals separated by the nostril, the loreal, the invariably single preocular, the eye, the postoculars (usually three but often two or four), and the temporals—a large anterior one followed by two, and these followed by two more. Below these plates are the supralabials (usually seven), of which the third and fourth are in contact with the eye; occasionally the number is increased to eight on one or both sides by division of the third. The infralabials are normally ten, occasionally nine, rarely eight or eleven. There are two pairs of genials of which the posterior are markedly longer than the anterior. Variation in numbers of postoculars, temporals, supralabials, and infralabials is mainly individual; if there are average differences in these characters between geographic populations, they must be very slight. Gastrosteges vary in number at least from 146 to 177. Males have, on the average, about five more gastrosteges than have females. Urosteges vary similarly and range from 70 to 94. There are always 19 scale rows on the body, but of these the fifth on each side drops out at about two-thirds of the distance from head to the anus, leaving only 17 rows on the posterior third of the body.

The only scale characters which have been demonstrated to vary geographically are numbers of gastrosteges and urosteges. In general, those populations which have the most gastrosteges also have high numbers of urosteges, and in those having reduced numbers of gastrosteges the urosteges are correspondingly fewer. This parallelism does not hold everywhere; the population from Mendocino County, California, is near the minimum in number of gastrosteges, but markedly exceeds some other populations in number of urosteges (see Figs. 1 and 2).

Owing to its greater variability, the color pattern of the species is less readily described than the scalation. The dorsal ground color may be black, gray, or brown. There is a bright yellow, longitudinal, middorsal stripe which covers, on the average, about 1 2/2 rows of scales, continuously from the nape nearly to the tip of the tail. Usually its borders are regular and sharply defined. The skin between scales of the dorsal stripe is dark. There is a pale lateral stripe on each side of the body, which normally includes all of the second

scale row and most of the third row. The lateral stripe is pale yellow, with less sharply defined borders than the dorsal stripe. The lateral stripe is usually separated from the pale ventral surface by a darker area on the first scale row and the lateral edges of the gastrosteges. This area may be solidly black, but more often there is merely a dusky suffusion of the scales. Above the lateral stripe a series of red blotches is superimposed on the ground color of the body. These blotches vary greatly in extent, both in individuals and in geographic populations; they are mainly confined to the skin between the scales, but they also overlap on the edges of the scales. Usually they are sharply defined and stand out against the dark ground color, but, in some specimens in which the ground color is pale, the red blotches blend into it, suffuse it, and are not sharply defined. Some of the anterior blotches may blend into the lateral stripe, suffusing it with reddish. The red blotches may be broken up and divided by black areas; often there is a second series of smaller blotches, placed above, and alternating with, the main blotches; there may even be three distinct series on each side. Usually the red marks are less extensive than the intervening areas of the dark ground color, but they may be so enlarged that the dorsal ground color is predominantly red, or they may even join, forming a longitudinally continuous red area between the dorsal and lateral stripes.

The ventral surface is pale yellowish gray, nearly white anteriorly, and gradually becoming more dusky posteriorly. It may be blotched or stippled with black, or it may be solid black posteriorly in heavily pigmented individuals. The top of the head may be black (passing into olive on the rostrum) or some shade of brown, gray, or red. On the side of the head, the nasals, the upper parts of the loreal and preocular, the upper postocular, and the temporals are usually dark, or at least match the color of the top of the head, but pass into pale olive or yellowish on the supralabials, the lower parts of the loreal and preocular, and the lower postoculars. There may be vertical black marks on the posterior parts of the supralabials, especially on those behind the eye. The supralabials may be suffused with dusky coloring on their upper parts.

All of these characters of color pattern are subject to much geographic variation, and also vary individually. However, there is apparently little or no sexual, seasonal, or age variation in color pattern. Small young resemble adults from the same localities in appearance except possibly for slightly paler ground color. Males and females within series from the same region are alike in color pattern or show about the same range of individual variation. Individuals kept in captivity for periods of months showed no change in shade or distribution of colors.

Accounts of Subspecies

THAMNOPHIS SIRTALIS PICKERINGII (Baird and Girard)

Eutainia pickeringii Baird and Girard, 1853:27.
Eutaenia pickeringii, Girard, 1858:150, pl. 13, figs. 14-20.
Eutaenia sirtalis tetrataenia Cope, 1875:546 (part).
Eutaenia sirtalis pickeringii, Cope, 1892:665.
Eutaenia sirtalis trilineata Cope, 1892:665 (part).
Thamnophis parietalis pickeringii, Van Denburgh, 1897:204.
Thamnophis sirtalis concinnus, Ruthven, 1908:173 (part).

Fig. 3. Map showing locality records for specimens examined of *Thamnophis sirtalis*; 1. *T. s. pickeringii*; 2. *T. s. concinnus*; 3. *T. s. tetrataenia*; 4. *T. s. infernalis*. Two far northern records of *tetrataenia*, Hazelton and Kispiox Valley, are not shown.

Diagnosis.—Top of head dark brown, sometimes black or nearly black in parietal region, paler on rostrum and temporals; dorsal stripe narrow, less than 1 2/2 scale rows wide and often confined to middorsal row, its borders irregular; dorsal ground color jet black; red lateral blotches small, inconspicuous, mainly confined to skin between scales; lateral stripe pale, whitish, conspicuous because bordered above and below by areas of solid black, its borders irregular, and skin between its scales black; ventral surface heavily marked with black, or solidly black posteriorly; supralabials pale with well developed black wedge-marks along their posterior borders.

Type.—The original description was based upon four specimens in the National Museum collected in the vicinity of Puget Sound, none of which has been selected as a lectotype.

Range.—Washington and southwestern British Columbia, including Vancouver Island.

Coloration.—Description of Mus. Vert. Zool. no. 16966, adult male from Bellingham, Whatcom County, Washington: Top of head uniform Brownish Olive on supraoculars, internasals, prefrontals, frontal, parietals, and temporals, paling on rostrum; sides of face

Grayish Olive on nasals, prefrontals, loreals, upper parts of supraoculars and upper parts of preoculars, paling to Sea-foam Green on lower parts of supralabials; preoculars, two lower postoculars, and anterior end of anterior temporal also Sea-foam Green but suffused with dusky pigment, as are the last two supralabials; distinct black wedge-marks on posterior parts of all supralabials; posterior gular scales and two posterior infralabials marked with black; chin yellowish white; ventral surface becoming increasingly tinted posteriorly, passing into Hathi Gray; ventral surface also increasingly dotted with black posteriorly; posterior third of body and tail solidly black ventrally; dorsal stripe Sulphur Yellow, 1 2/2 scale rows wide at anterior end of body, narrower posteriorly and involving only inner parts of scales on either side of middorsal row; anterior edges of scales in middorsal row and skin between scales black; edges of dorsal stripe thus broken and irregular; dorsal color black; red lateral marks inconspicuous, confined to area between third and upper half of seventh scale rows on each side, successive marks separated by intervening black areas equal to or exceeding length of a scale; each red mark equal to length of about half a scale, but broken and irregular, and mainly confined to skin between scales and edges of scales; lateral stripe confined to second and lower part of third scale rows, slightly wider on anterior part of body than on posterior part, its borders irregular and edges of its scales and skin between them black; lateral stripe bordered below by solid black area on first scale row and lateral corners of gastrosteges.

Comparisons.—Differs from other races in narrowness of dorsal stripe, which is often confined to middorsal scale row, whereas in other forms it usually includes from 1 2/2 to 3 rows; in uneven or irregular edges of dorsal stripe, which in other subspecies has even, straight, and sharply defined edges; in presence on posterior parts of supralabial scales of wedge-shaped black marks, which in other races are entirely absent or are reduced and present on only one or two posterior supralabials; in black edgings of scales of pale lateral stripe, edgings usually are absent in other races. In *pickeringii* the head is mainly dark brown on top, thus differing from *concinnus* and *infernalis* which have pale and mainly reddish heads, and also from most *tetrataenia* in which the head is usually black. In its jet black dorsal ground color *pickeringii* differs from *infernalis*. In the possession of heavy black markings or solid black posteriorly on the ventral surface it differs from *tetrataenia* and *infernalis*, which are pale ventrally, and resembles *concinnus*, but its melanism is more extreme.

Variation.—Specimens from the Olympic Peninsula and the east side of Puget Sound all have the characters of typical *pickeringii* strongly developed, with narrow dorsal stripes, dark brown heads, distinct supralabial wedge-marks, and heavy ventral pigmentation. The head of *pickeringii* appears to be proportioned somewhat differently from the heads of the other kinds of *sirtalis* studied, being narrow posteriorly and having especially large eyes. All *pickeringii* examined were far below the maximum sizes attained by the other subspecies, perhaps indicating that *pickeringii* is genetically a small race.

Specimens from Alberni Valley, Vancouver Island, British Columbia, are typical in most respects. One (Mus. Vert. Zool. no. 2307) has the lateral red

marks large and conspicuous, but they are small and hardly noticeable in eight others of the same series. All have heavy black ventral markings, narrow dorsal stripes, and supralabial wedge-marks.

Two from Lillooet River Valley, British Columbia, are nearest *pickeringii*, but seem to show intergradation with *tetrataenia*, which they resemble especially in having but little ventral pigmentation. One from Union Bay, Bayne Sound, on the east side of Vancouver Island (Stanford no. 7212), differs greatly from typical *pickeringii* in having the dorsal ground color dull brown on head and body, with no red lateral marks showing; also, supralabial wedge-marks and black ventral pigmentation are lacking, and the dorsal stripe is wide — slightly more than 1 2/2 scale rows.

Specimens from farther east and those from farther north, even in the coastal region (Calvert Island, Hazelton, Kispiox Valley), do not show the subspecific characters of *pickeringii*, and are here referred to *tetrataenia*.

The only *sirtalis* examined from Washington east of the Cascade Range were three from Pullman, Whitman County, in the extreme eastern part of the state. These have dark brown heads, distinct supralabial wedge-marks, and scattered black markings ventrally. Thus they resemble *pickeringii* more than they resemble *tetrataenia*, and they seem to indicate that the subspecies *pickeringii* ranges eastward across the entire state of Washington.

THAMNOPHIS SIRTALIS CONCINNUS (Hallowell)

Tropidonotus concinnus Hallowell, 1852:182.
Eutaenia sirtalis obscura, Cope, 1875:41 (part).
Eutaenia sirtalis concinna, Cope, 1892:664.
Thamnophis sirtalis concinnus, Ruthven, 1908:173.

Diagnosis.—Top of head and face, including supralabials and infralabials, predominantly red; dorsal stripe pale yellow, narrow (1 2/2 scale rows wide), with even and sharply defined borders; dorsal ground color jet black; red lateral blotches sharply contrasted with ground color and in a single series; red blotches small, usually not more than one-third as long as black areas separating them; lateral stripes narrow, pale milky yellow, with irregular borders, bounded below by jet black areas that set them off, or else partly or entirely absent; ventral surface heavily marked with black, often in extensively continuous areas, superimposed on pale blue background.

Type.—Adult female, Phila. Acad. Sci. no. 6324; collected in "Oregon" [probably in the lower Willamette Valley] by Dr. B. F. Shumard.

Range.—Drainage basin of Willamette River, and coastal region of northern half of Oregon.

Coloration.—Description of Mus. Vert. Zool. no. 25314, adult female, from three miles east of Corvallis, Linn County, Oregon: Head Flesh-Ocher, marked with black along inner parts of parietals and around edges of frontal, somewhat suffused with dusky brownish pigment on top, and to a lesser extent on upper parts of supralabials, preocular, loreal, and nasals; infralabials reddish, chin mainly white; dorsal stripe Ivory Yellow, 1 2/2 scale rows wide,

sharply defined by regular edges, somewhat suffused with reddish at anterior end; ventral surface solidly black on posterior half of body; chin whitish, passing into Tilleul-Buff on anterior gastrosteges, and into Pale King's Blue; first four gastrosteges without black marks; more posterior ones solidly black laterally and increasingly mottled medially, until black is predominating color at about one-fourth distance from head to anus, this darkening increasing posteriorly, to total exclusion of pale color at about mid-body; almost continuous irregular, pale, bluish markings along mid-ventral surface of tail; dorsal ground color jet black, with about 75 Flesh-Ocher blotches on each side on area extending from second to sixth scale rows inclusive, each blotch about 3 1/2 scales high and one scale long; color of blotches brighter on skin between scales, slightly suffused with dark ground color on scales themselves; successive boltches separated by distance of about 1 1/2 scales; no lateral stripes.

Comparisons.—Resembles *infernalis* in having red head, but head of *concinnus* usually brighter, less suffused with gray. Differs from *infernalis* in jet black rather than brown or gray dorsal ground color and in narrower dorsal stripe (not more than 1 2/2 scale rows wide); red markings on sides sharply contrasted with ground color instead of blended with it, small and widely separated in contrast to enlarged markings of *infernalis*, which often join to form continuous red area along side; lateral stripes absent or narrow, and bounded below by solid black area, whereas in *infernalis* lateral stripes are wider and may be bounded below merely by a dusky area; posterior ventral surface heavily marked with black, or solidly black, in contrast to pale ventral surface of *infernalis*.

Differs from *tetrataenia* in red rather than black, brown, or gray head; in slightly narrower dorsal stripe (on the average); in frequent lack of lateral stripe; in heavily pigmented rather than pale ventral surface.

Variation.—*T. s. concinnus* has its racial characters most strongly developed in the Willamette Valley in west-central Oregon. Apparently in this region the transition from *concinnus* to *tetrataenia* farther south in the Umpqua basin is abrupt, and the low divide separating the Umpqua and Willamette river drainages may act as a barrier keeping these populations distinct.

A specimen from Deadwood, near the coast in Lane County, may be considered an intergrade between *concinnus* and *tetrataenia*. The head is reddish, suffused with brown, and is marked with black on the parietals and frontal, but the supralabials are pale, with reddish suffusion only on the last one. There is only a little black pigmentation ventrally; the lateral stripe is bordered below by a continuous black area. At Siltcoos Lake, only about 25 miles southwest of Deadwood, numerous *sirtalis* seen in the field appeared to be typical *tetrataenia*.

Other snakes from farther north in the coastal region, at Alsea, Benton County, and between Chitwood and Siletz River, Lincoln County, are good *concinnus* in most respects, but are not typical in that they have no heavy black markings. Eight individuals from Tillamook and one from Garibaldi,

Tillamook County, show the characters of *concinnus*, but these are less strongly developed than in the snakes of the Willamette Valley. All have the heads red on top, but some are heavily marked with black in the parietal region. Some have ventral surfaces pale and nearly immaculate, whereas others are speckled with black posteriorly. One from Yamhill County between Grand Ronde and Dolph has the characters of *concinnus* strongly developed; it lacks lateral stripes, and has a bright red head and heavy ventral pigmentation. In four from Gearhart, Clatsop County, extreme northwestern Oregon, the heads are dull and brownish on top, with black marks on the parietals, and the ventral surfaces are mainly pale. In two from Olney, only a few miles from Gearhart, the heads are distinctly reddish and the ventral surfaces are mottled with slate posteriorly. No Washington specimens were seen which had the characters of this race well developed, therefore the range of *concinnus* is thought to include only northwestern Oregon.

Remarks on systematics.—From the original description of the type, and a subsequent fuller description by Baird and Girard (1853:146), it is evident that this specimen was one having the distinctive characters of the subspecies well developed. Thus the jet black dorsal ground color, the pale dorsal stripe, the small size of the red lateral spots, the "greenish black ventral surface tinged with white anteriorly," the absence of lateral stripes, and the reddish yellow color of the head are mentioned. The type locality given was merely "Oregon," and no date accompanied the specimen. Although many of the specimens in early collections that were labeled "Oregon" were from within the boundaries of the present state of Washington, it is evident that the type of *concinnus* actually came from Oregon. I can find no record of Shumard's travels, but in the Proceedings of the Philadelphia Academy of Sciences under date of January 6, 1852 (p. 1) it is recorded that a letter sent by Shumard from Oregon City, November 18, 1851, giving an account of his geological observations in Oregon Territory was read before the Academy. Oregon City is in the lower Willamette Valley, within the range of *concinnus*, and it seems quite probable that the type came from there.

T. s. concinnus is abundant in the upper Willamette Valley and in that region its racial characters are strongly developed. During several years residence at Eugene, Lane County, Oregon, the writer was familiar with this form and knew it to be distinct from *sirtalis* of southwestern Oregon (a population of *tetrataenia*, which heretofore has been included with *concinnus*), since living individuals are strikingly different in color and pattern.

Though many specimens from the Willamette Valley have distinct lateral stripes, there is a strong tendency for them to be suppressed by a filling in of this area on the sides with the jet black ground color.

Ruthven (1908:175) examined a series of nine specimens from Portland, Oregon, all of which had this style of coloration. He pointed out the difference between this style of coloration and the *pickeringii* style of western Washington in which the lateral stripes are present, there is no red on the head, and the dorsal stripe is narrow and confined to the middorsal row of scales. Although Ruthven recognized the fact that populations having these two

pattern schemes occupied distinct geographic ranges, he did not regard them as racially distinct, but stated that the two had in common a tendency for increase in amount of black pigment, and that the differences between them were too slight to justify their subspecific separation.

Despite the fact that no differences in scalation are apparent between these two populations, their striking and fairly constant differences in color pattern would seem to justify their assignment to separate subspecies.

Thamnophis sirtalis tetrataenia (Yarrow)

Eutaenia infernalis, Girard, 1858:148.
Eutainia concinna, Lord, 1866:306.
Eutaenia sirtalis tetrataenia Yarrow, 1875:546 (original description).
Eutaenia sirtalis sirtalis, Cope, 1875:41 (part).
Eutaenia sirtalis parietalis, Cope, 1875:41 (part).
Eutaenia sirtalis obscura, Cope, 1875:41 (part).
Eutaenia sirtalis dorsalis, Cope, 1875:41 (part).
Eutaenia sirtalis pickeringii, Cope, 1875:41 (part).
Thamnophis sirtalis parietalis, Yarrow and Henshaw, 1878:1638.
Tropidonotus sirtalis infernalis, Garman, 1883:25 (part).
Eutaenia sirtalis, Townsend, 1887:240.
Tropidonotus ordinatus var. *infernalis*, Boulenger, 1893:214.
Thamnophis parietalis, Stejneger, 1893:214.

Diagnosis.—Top of head black or very dark brown posteriorly, with iridescent luster, paling to olive on internasals and rostral; dorsal stripe bright yellow, usually about 1 2/2 scale rows wide, its borders regular and sharply defined; dorsal ground color jet black, or nearly black suffused with brown or gray; red markings on sides conspicuous, usually shorter than black interspaces; lateral stripe dull yellow, including second scale row and most of third; stripe bordered below by dusky brown (or rarely solidly black) area involving first scale row and lateral edges of gastrosteges; ventral surface pale, yellowish gray, immaculate or sparingly marked with black posteriorly; supralabials suffused with dusky coloration on their upper parts, pale yellowish below, lacking conspicuous black markings.

Type.—U. S. Nat. Mus. no. 21384 (originally no. 866); collected at "Banks of Pit River, California" by Dr. J. S. Newberry.

Range.—British Columbia except extreme northern and southwestern parts; Washington and Oregon east of Cascade Range, extending westward to coast in southern half of Oregon; Great Valley and Sierra Nevada of California, west to coast in northern part of state, and through Trinity, eastern Mendocino, and Lake counties farther south; northern California east of Sierra Nevada, extending into state of Nevada along Truckee and Carson river drainages.

Coloration.—Description of Mus. Vert. Zool. no. 21222, adult female, from near McArthur, Pit River, Shasta County, California: Top of head black posteriorly on temporals, parietals, frontal, and supraoculars (except for anterior corners), but passing into Deep Grayish Olive at anterior ends of supraoculars and on prefrontals, internasals, and rostral; paling into Light Grayish

Olive on nasals, loreal, preoculars, postoculars, anterior portion of first temporal, scales behind corner of mouth, all of supralabials (except their lower portions which are white), and last infralabial; a slender vertical black mark along posterior edge of fifth supralabial; ventral surface white anteriorly on chin, blending into Puritan Gray [Pale Olive-Buff in no. 21220 from same locality] on gastrosteges (perhaps slightly stained by preservative) and laterally on urosteges; an irregular midventral white area on tail, narrow just behind anus, but broadening posteriorly almost to exclusion of gray; dorsal ground color black; dorsal stripe Sulphur Yellow, somewhat suffused with brownish, especially posteriorly; lateral stripe dull, Light Olive-Gray, confined to second scale row and lower half of third; red blotches on sides Coral Red, mainly confined to skin between scales, and restricted to area of third, fourth, and fifth scale rows, each blotch wholly or partly divided into upper and lower portions by scales of fourth row; about one pair of blotches for every other transverse row on anterior part of body; lateral stripe bordered below by area of Dark Grayish Olive involving first scale row and lateral edges of gastrosteges.

Comparisons.—Differs from *infernalis* in predominantly black (or dark brown) rather than red or grayish color of head; in black or nearly black dorsal ground color (in *infernalis* black is mainly restricted to areas bordering dorsal stripe, giving way to paler color farther down on sides); in usually less extensive red lateral markings which are well separated; and in slightly narrower dorsal stripe on the average (last two characters subject to considerable individual variation with overlapping between forms).

Variation.—This race, as understood by me, has a much greater geographic range than the other races here considered. Correspondingly, it shows more geographic variation as a subspecies, and several of its populations compared with each other show slight but fairly constant differences.

Six specimens from Hazelton and Kispiox Valley, western British Columbia, apparently constitute the northernmost record for reptiles on the North American continent. They are not typical of *tetrataenia* and tend to resemble *pickeringii* in increased extent of black pigmentation. The dorsal stripes in some are narrow (less than 1 2/2 scale rows wide), the lateral stripes are bordered by continuous black areas below, and the ventral surface is sparingly dotted with black medially on the posterior part of the body and tail. These specimens have no distinct supralabial wedge-marks. Red marks on the sides are small and inconspicuous; they tend to be broken up and are suffused with the ground color.

A single specimen from Calvert Island (Mus. Vert. Zool. no. 17968) also has the red lateral marks broken up, but they are larger and more conspicuous. This specimen has the black areas below the lateral stripes discontinuous and broken up into series of spots, and the ventral surface is heavily dotted with black posteriorly. The plates on top of the head and the temporal scales are mainly red in this specimen, but the parietals are heavily marked with black. It is the only red-headed specimen here referred to *tetrataenia*, except one or two *concinnus* intergrades from the Oregon coast. Its locality is far removed

from the ranges of the red-headed races *concinnus* and *infernalis*, and in other respects it differs from both in its color pattern. It may be merely an unusual individual variant, or it may be typical of an insular population having well differentiated color pattern characters.

These anomalous specimens from the coastal region of British Columbia are doubtfully referred to the subspecies *tetrataenia*. Series from the interior of British Columbia are more nearly typical, although all differ in appearance from Californian specimens. In seven from the vicinity of Vernon the coloration is peculiar in that the head (which is dark brown, nearly black on top) is tinted with red on its sides, behind the nostril, on the upper part of the preocular, on the upper postoculars, and around the corner of the mouth. The temporals are paler than the general shade on top of the head, and, in several, are marked with red in the centers of the scales. The dorsal ground color is black. Others from Creston, Monashee Mountain, Bridge River at Minto Mine, and Crayton Valley are similar in appearance.

Numerous Idaho specimens (Eagle, McCall, Boise, Weiser) have the head and body dark brown rather than black dorsally, and some have a reddish suffusion on the side of the head; others from Blue Lakes, Twin Falls County, in the southern part of the state, have a black ground color and resemble specimens from southern Oregon and California, except that the red lateral spots tend to be more broken, and in some the lateral stripe is accentuated by the black (instead of brownish) area bordering it below. Some have scattered blackish markings on the posterior ventral surface.

One from Austin, Grant County, Oregon, also has a reddish suffusion on the side of the head, and the head is black on top. This tendency to develop a reddish suffusion on the side of the head may be widespread in the northeastern part of the range of *tetrataenia*.

Specimens from southern Oregon, from the basins of the Klamath and Rogue rivers, are, to me, indistinguishable, except that those from the Klamath region seem to attain considerably larger maximum size. In all individuals the ground color is black on the body and the top of the head, passing into pale olive in the rostral region. The supralabials are not marked, but are dull and are suffused with dusky pigment on their upper parts. The ventral surface is immaculate, pale yellow, nearly white on the chin, becoming dusky posteriorly and passing into pale gray. The lateral stripe is bordered below by an area suffused with dull brown on the first scale row and lateral edges of the gastrosteges.

Numerous specimens from the coast of Curry and Coos counties, Oregon, and Del Norte County, California, differ from those described above in having a faint reddish suffusion on the sides of the head, and they may have the top of the head dark brown rather than black. Some have a black area bordering the lateral stripe below. One in a series of twenty from Myrtle Point, Coos County, deviates from the above description in having the top of the head and the labials mainly red. In one from Tahkenitch Lake, Douglas County, the side of the head is conspicuously tinted with red, and the ventral surface

is heavily dotted with black on the posterior part of the body and on the tail. The top of the head is brownish, even on the frontal and parietal plates. This specimen differs in coloration from typical *tetrataenia* in the direction of *concinnus*, the range of which it also approaches. In specimens from Deschutes and Lake counties, Oregon, and from Modoc, Lassen, and Siskiyou counties, California, there is no red on the head, which tends to be dark brown rather than black on top, and the lateral stripe is bordered below by a dull brownish suffusion rather than by a black area.

In numerous specimens from the Sacramento Valley and Sierra Nevada the head is usually dark olive or brown rather than black on top, and the lateral stripe is almost continuous with the pale color of the ventral surface, having the dusky suffusion along its lower border extremely faint. None has any red either on the top or on the sides of the head. The same remarks apply to San Joaquin Valley specimens. In five from Kern County the ground color is dark gray rather than black, and the keels and centers of the scales are pale. These specimens thus tend to resemble the pale southern population of *infernalis* south of the Tehachapi Range and may be considered intergrades between it and typical *tetrataenia*.

Remarks on systematics. — The three specimens upon which the name *tetrataenia* was based were abnormal in coloration, having the red blotches fused longitudinally to form a continuous red band on each side, bounded above and below by black areas. I have seen no specimens having this pattern, which must be very unusual and of sporadic occurrence in the range of the species. The three specimens listed by Cope (1892) belong to two different subspecies.

The name *tetrataenia* first appeared in a report by Yarrow (1875) in a key to the garter snakes of the southwestern states — thus a diagnosis of sorts was provided though no range was indicated, no actual specimens were mentioned, and the name appeared only once in the paper. It is obvious that Yarrow did not intend to describe *tetrataenia* as a new form; at the beginning of his discussion of the garter snakes he expresses his indebtedness to Cope for assistance with this group; he mentions having access to Cope's manuscript wherein new forms were described, and part of the discussion (but not the key) is in quotation marks. Evidently he expected Cope's manuscript to be published before his own paper.

Later, in the same year, Cope's "Check-list of North American Batrachia and Reptilia" was published, and in it the name *tetrataenia* appears, with the citation "Cope MS." and a statement of the range, "Pit River, California." The actual description by Cope did not appear until 1892; doubtless it had undergone some modification and additions had been made, before its long delayed publication was effected. Three specimens were mentioned in this description, two from Pit River, California, both catalogued as U. S. Nat. Mus. no. 866, and one from Puget Sound. According to Brown (1903:292) this Puget Sound specimen is catalogued as no. 6085 in the collection of the Philadelphia Academy of Sciences.

Dr. L. Stejneger of the United States National Museum has, at my request, kindly reinvestigated the type material of *tetrataenia* there and has furnished important information regarding it. It is apparent that the descriptions by Cope in 1892 and 1900 were composites based on more than one specimen. The Puget Sound specimen mentioned is not now in the National Museum according to Dr. Stejneger. It is probable that the scale counts given in Cope's description — gastrosteges 158, urosteges 68 — were based on this Puget Sound specimen since they do not agree well with counts for either of the Pit River specimens (164, 10; 162, 86). The measurements in Cope's description — total length 800 mm., tail (tip lost) 118 mm. — do not agree well with either of the Pit River specimens (800 mm., 37 mm.; 670 mm., 180 mm.) or with the accompanying statement "length of tail entering total length four and one-fifth times." Dr. Stejneger is of the opinion that the smaller of the two Pit River specimens, no. 21384, is the one figured by Cope (1900, p. 1080).

Both Cope (1875:4) who actually discovered the abnormal pattern phase *"tetrataenia"* and Yarrow (1883:128), after he had published the original description, mentioned Pit River as the habitat of the form in publications prior to that in which mention of the Puget Sound specimen and locality first appear (Cope, 1892:664). It therefore seems extremely doubtful that this Puget Sound specimen was used at the time the original description was drawn up. Hence it may not be type material, although probably Cope's descriptions of 1892 and 1900 were in part based upon it.

On the other hand, the two Pit River specimens (nos. 21383 and 21384, renumbered by Stejneger, both originally no. 866) undoubtedly are the ones examined by Cope and Yarrow, and they agree with Cope's description (as I am informed by Dr. Stejneger) except for the discrepancies in scale counts and measurements indicated above. One of these, no. 21384, has therefore been selected as the lectotype.

THAMNOPHIS SIRTALIS INFERNALIS (Blainville)

Coluber infernalis Blainville, 1853:291, pl. 26, figs. 3 and 3a (original description).
Eutaenia imperialis Coues and Yarrow, 1878:280.
Tropidonotus sirtalis parietalis, Garman, 1883:25.
Eutaenia infernalis, Bocourt, 1892:40 (part).
Tropidonotus ordinatus var. *infernalis*, Boulenger, 1893:207 (part).
Thamnophis parietalis, Van Denburgh, 1897:200 (part).
Thamnophis sirtalis infernalis, Van Denburgh and Slevin, 1918:198 (part).

Diagnosis.—Top of head, and face including supralabials and infralabials, predominantly reddish; dorsal stripe bright yellow, broad (more than 1 2/2 scale rows wide), with even and sharply defined borders; dorsal ground color black in area adjacent to lateral stripe, but paling to gray or brownish farther down on sides; red markings on sides extensive and conspicuous, usually as long as interspaces, extending dorsally to within one or two rows of dorsal stripe, tending to suffuse and blend into adjacent pale ground color; lateral stripes well developed, bordered below by black or dusky area on first scale row and edges of gastrosteges; ventral surface mainly pale, immaculate or sparingly marked with black posteriorly.

Type.—Adult; Paris Museum d'Histoire Naturelle; collected in "Californie" [probably within the present boundaries of Sonoma, Marin, San Francisco, or Santa Clara counties] in 1827 or 1828, by Dr. P. E. Botta.

Range.—Coastal region of California, from Humboldt County south to San Diego County.

Coloration. — Description of Mus. Vert. Zool. no. 7618, adult from Nicasio, Marin County, California: Top of head Vinaceous-Buff, paling laterally to Yellowish Glaucous on supralabials; lateral stripe and ventral surface Yellowish Glaucous; dorsal stripe Sea-foam Yellow, three scale rows wide at its anterior end, slightly narrower posteriorly, with black encroaching on outer edges of its lateral scales; ventral surface of body immaculate; ventral surface of tail dotted with black medially; many of dark dorsal scales dotted with pale color; red blotches on sides Buff-Pink, each about one scale long, involving upper halves of scales of third row and all of those of fourth, fifth, and sixth rows; blotches nearly as long as black intervals between them, somewhat suffused with dark ground color, and not sharply delimited; on posterior part of body successive blotches tend to join by longitudinal connecting marks on fifth and sixth scale rows.

Variation.—The subspecies *infernalis* seems not to occur in typical form north of Sonoma County, California, but populations from western Mendocino and Humboldt counties are referred to it here because they are more like typical *infernalis* than typical *tetrataenia.*

Series from Del Norte County may be considered as intergrades. In one from Crescent City (Calif. Acad. Sci. no. 29222) the head is mainly red, with black markings on the parietals, and the ground color is dark grayish brown with keels on the scales pale, thus resembling *infernalis.* However, in nine others from the same locality, the heads are dark brown with only traces of red, this behind the nostril, in front of and behind the eye, and at the corner of the mouth; the ground color is dark, nearly black, and the red lateral marks are variable in extent. On the whole they are nearer *tetrataenia.*

Seven from Requa, at the mouth of the Klamath River, are similar in appearance but tend toward *infernalis* more strongly in having the tops of the heads reddish brown or chocolate brown, the ground color dark brown, and the red lateral marks not sharply set off from the ground color. In specimens from localities in western Humboldt County, the heads are pale, reddish, suffused with brown or gray, with the supralabials distinctly paler and grayer than the top of the head; the ground color is brown or gray, or nearly black, with superimposed darker areas creating a spotted appearance; red lateral marks are not especially enlarged and do not fuse to form continuous red areas on the sides, as they often do in typical *infernalis;* the dorsal stripe is often more than 1 2/2 scale rows wide.

Several from eastern Mendocino County agree with *tetrataenia* in all respects, but others from various localities in western Mendocino County have

the ground color dull brown rather than black, the tops of heads reddish brown or gray, the sides somewhat suffused with the reddish color of the lateral blotches, and the supralabials of a dull tone resembling the top of the head. They thus tend toward typical *infernalis* but differ from it in the less extensive red markings on the sides and in the duller color of the tops of the heads, which are usually grayish or brownish rather than bright red.

Even within Sonoma and Marin counties, there seems to be local variation in color, and some specimens have dull, grayish heads. The most brilliantly colored specimens are those from the immediate vicinity of the seacoast, especially those from the Point Reyes Peninsula.

In one from Berkeley, Alameda County, on the east side of San Francisco Bay, the top of the head is duller and more grayish (probably somewhat suffused with reddish in life) and the ground color is dark. One from Walnut Creek, Contra Costa County, has a grayish olive head and dark ground color, and hence it approaches *tetrataenia*.

Many specimens examined from the vicinity of Palo Alto, Santa Clara County, have pale, grayish brown heads, but all had been in preservative many years and probably the heads had faded from a color that originally was red. Several living *sirtalis* from the vicinity of Palo Alto all had red heads. Snakes of the Palo Alto series all have broad dorsal stripes — as much as three rows wide anteriorly and only slightly narrower on the posterior part of the body. Two scale rows on each side of the dorsal stripe are black except for pale keels; farther down on the sides the ground color pales to gray, with large red blotches which are often more extensive than the interspaces and tend to blend into the ground color; in some these red blotches tend to fuse longitudinally. A series of lateral black spots occurs on the third, fourth, and fifth scale rows, centering mainly on scales of the fourth row: each spot is about 1 1/2 scale rows long and two scales high, is irregular, and the scales show pale keels. Successive spots are separated by a distance of about 1 1/2 scales.

One specimen from Pacific Grove, Monterey County, also fits the above description; a second from the same locality has a darker ground color. Numerous specimens from San Benito County have dark ground color, with heads black on top; these should be referred to *tetrataenia*. None is available from the vicinity of the seacoast in southern Monterey, San Luis Obispo, or Ventura counties.

Specimens from south of the Tehachapi Range differ from others in having much paler ground colors, and this tendency is more pronounced in some from the San Bernardino Mountains than in those from Santa Barbara and Los Angeles counties. In these southern specimens the heads are pale, grayish brown on top and marked with black in the parietal region; the dorsal stripe is bright yellow and about 1 2/2 scale rows wide, with regular and sharply defined borders; the body ground color is pale gray, with two rows of small, black spots on each side which are well separated; the red lateral marks are small and shorter than the intervening areas.

Remarks on systematics.—The type of *infernalis* was described by Blainville (1835:291, pl. 26, figs. 3 and 3a), but no more specific locality than "Californie" was given. Few characters of diagnostic importance were mentioned in the brief description, and the crude figures, including a color plate, do not agree with the description or with any known snake.

Some doubt has therefore existed among herpetologists as to the applicability of this name. Baird and Girard (1853, p. 26) were the first American authors to recognize *infernalis* and they applied the name to a garter snake of the species *sirtalis* from central California. Thereafter the name was frequently applied to snakes of the species *sirtalis* from California and adjacent regions, but also to a form of the *ordinoides* complex which likewise occurs in western California, and for which the name *atratus* is now generally accepted.

Thamnophis ordinoides atratus resembles *sirtalis* in several respects more than do other members of the *ordinoides* group. It has only nineteen scale rows, occasionally has only seven pairs of supralabials, and further resembles *sirtalis* in having red spots, which are lacking in other races of *ordinoides* in the dark dorsolateral area. The original description did not describe scalation or coloration in sufficient detail to permit positive identification of the type.

Bocourt (1892:40) gives some further information regarding the type, stating that it has nineteen scale rows and seven pairs of supralabials. *T. o. atratus* normally has eight pairs of supralabials, and though occasionally the number is reduced to seven on one side, it is only rarely reduced on both sides. In the colored plate accompanying the original description, the head is of a brownish gray color, contrasting with the dark color of the body. In this respect the coloration seems to resemble that of faded specimens of the red-headed coastal populations of *sirtalis*, but differs from that of *atratus* in which the ground color is the same on the head and body.

In the original description the total length was given as .84 m. of which the tail comprised .16 m. (leaving .68 m. as the head and body length). In the large series of *atratus* examined by me, 44 were considered to be adults, and of these the largest had a head and body length of 59 cm. (thus it was considerably smaller than the type of *infernalis*). As compared with other garter snakes, *atratus* is a relatively small race, but the species *sirtalis* attains much larger size, and the measurements given fall within its normal size range. These data seem to indicate that the application of the name *infernalis* to a race of the species *sirtalis* is correct and that its application to a member of the *ordinoides* group was erroneous.

The type of *infernalis* was collected by Dr. Paolo Emilo Botta along with other California reptiles, including the types of *Phrynosoma coronatum, Gerrhonotus multi-carinatus, Charina bottae, Pituophis catenifer, Lampropeltis getulus californiae*. Botta was surgeon on the French ship, "Le Heros." Palmer (1917) has published a brief account of Botta's visit to California, showing that he stopped at many places along the California coast from Bodega and Ross to San Diego, and including Solano, San Francisco, Santa Clara, San Jose, Santa Cruz, Monterey, Santa Barbara, San Gabriel, Los Angeles, and

San Pedro. The type of *infernalis* might have been collected at almost any one of these places.

Summary and Discussion

The wide-ranging species *Thamnophis sirtalis* has four geographic races in the Pacific Coast region of North America. These are separable mainly on the basis of color characters, but there are also continuous trends in numbers of gastrosteges and urosteges, so that populations at opposite extremes of the range of the species differ markedly in numbers of these scales.

Thamnophis sirtalis pickeringii of Washington, and British Columbia west of the Cascade Range, is characterized by having a narrow dorsal stripe, mainly confined to the middorsal scale row, black "wedge-marks" on the supralabials, and heavy black pigmentation on the ventral surface. *T. s. concinnus*, in the northern half of Oregon west of the Cascade Range, has a bright red head, a jet black dorsal ground color, lateral stripes reduced or absent, and heavy black ventral pigmentation. *T. s. tetrataenia* ranges over much of British Columbia. Washington, and Oregon, east of the Cascade Range, reaches the coast in southern Oregon, and occurs throughout the Great Valley, inner coast ranges, and Sierra Nevada of California; it has a black or nearly black ground color, no red on top of the head, little or no black pigmentation ventrally, and lateral stripes bordered below by a dull, brownish suffusion. *T. s. infernalis* of the California coast has a pale, red or reddish brown head, a broad dorsal stripe, enlarged red blotches on the sides, a pale ground color, and little or no black ventral pigmentation.

No significant geographic variation could be found in number or arrangement of head scales, or in number or relative length of scale rows on the body, although there is much variation in these characters in the *ordinoides* artenkreis of the same genus which occurs over the same area. In this region characters of color pattern vary less in the *sirtalis* group than in the *ordinoides* group. These characters are especially valuable in *sirtalis* nevertheless because in them geographic trends are better defined and less obscured by individual variation than in scale characters.

In the kinds of *sirtalis* studied, the only scale characters which show marked geographic variation are numbers of gastrosteges and urosteges; both decrease progressively in numbers from the southern to the northern extremes of the range. Although this trend is, for the most part, quite gradual, the transition is abrupt between some adjacent populations that are separated by barriers, notably the populations on the north and south sides of San Francisco Bay. Also there is a tendency for inland populations to exceed those of the immediate coastal region in numbers of gastrosteges and urosteges. This variation closely parallels variation in the *ordinoides* group in which all far northern, coastal, or isolated high mountain populations are exceeded in numbers of gastrosteges and urosteges by their nearest relatives occurring farther south, farther inland, or at lower altitudes, respectively. In the *ordinoides* group reduction in numbers of these scales is characteristically accompanied by genetic dwarfing in body size. It is quite probable that the same kind of dwarfing

accompanies reduction in gastrostege numbers in *sirtalis*, although this cannot be well shown with the smaller series available.

The largest *sirtalis* examined were from the Klamath Lakes region and the San Joaquin Valley. Series from these same areas have relatively high numbers of gastrosteges and urosteges. The largest races of *ordinoides* are endemic to these areas, hence it appears probable that the environment in these regions of extensive swamp lands and hot summer climates favors large size in garter snakes. All *sirtalis* of the northwestern race *pickeringii* that were examined were small, and in the area inhabited by them the smallest members of the *ordinoides* complex (the subspecies *ordinoides*) occurs. A local population of *Thamnophis ordinoides vagrans* in the same region is markedly smaller than typical *vagrans* of the Great Basin. Judging from these data, it appears that, in general, *Thamnophis sirtalis* shows the same correlations between numbers of ventral scales and body size, and between body size and climate, which are apparent in *Thamnophis ordinoides*.

Study of the *ordinoides* complex has resulted in the conclusion that color pattern is less influenced by climatic and other physical conditions than by biotic factors in the special ecologic niches occupied. Therefore parallel geographic trends throughout the ranges of *sirtalis* and *ordinoides* could hardly be expected. In keeping with its more stable ecologic niche, *sirtalis* varies much less in color and pattern than does *ordinoides*. *T. sirtalis*, judging from my field experience with it, is preëminently a marsh- or meadow-inhabiting species. Everywhere that it occurs it seems to favor a habitat of thick vegetation in damp places, unlike some races of *ordinoides* which seem to be well adapted for foraging under water in swift streams *(couchii, hydrophila)*, or in dry situations away from the water *(elegans, hueyi)*. In the *ordinoides* group it was found that those forms which characteristically forage in dense vegetation *(atratus, elegans)* have bright and sharply defined dorsal stripes set off against a dark ground color, whereas those races which tend to forage in other situations may have the dorsal stripe dull *(biscutatus)*, faint and poorly defined *(vagrans, couchii, hydrophila)* or wanting *(hammondii, digueti)*, and may have pale ground color with spotted or checkered patterns.

In line with this idea is the fact that *sirtalis* always has a bright yellow dorsal stripe, which is usually more sharply defined and shows more regular borders than in any member of the *ordinoides* group. This pattern scheme of a bright, dorsal stripe set off against a dark ground color is thought to have protective value, especially in a habitat of thick vegetation; the longitudinal continuity of color disguises motion as the snake glides through grass or brush with only part of its body visible. This part seems to shrink and vanish before the eyes of the observer, who may not be aware that it is in motion, or at least may not detect the direction and rate of motion, as he would if there were conspicuous transverse markings. As a species, *sirtalis* in its coloration seems protectively adapted for foraging in high grass or riparian thickets.

In western Washington the *sirtalis pickeringii* type of pattern, with dark brown head, jet black dorsal ground color, narrow, pale yellow, lateral stripes with irregular borders, and ventral surface heavily marked with black, is

remarkably paralleled by individuals of *Thamnophis ordinoides ordinoides*. In more southern parts of its range, the subspecies *ordinoides* does not have this pattern; the dorsal stripe is wider and may be red or orange, or may be suffused with the ground color, or even entirely wanting; the ground color is usually brown, and there is little or no black ventrally. The third kind of garter snake inhabiting the Puget Sound region, *T. o. vagrans*, also has heavy ventral pigmentation and shows darker ground color here than it does in the more southern and eastern parts of its range in the Great Basin.

The characteristic color pattern of *sirtalis concinnus* in western Oregon has no close counterpart in the *ordinoides* group, although the subspecies *ordinoides* ranges over the same general area and occurs in the same habitats. *T. o. ordinoides* has a paler ground color in this part of its range and often has a red or orange stripe. Certain individuals of *T. o. atratus* from the San Francisco Peninsula resemble *concinnus* in having heavy pigmentation and jet black dorsal ground color, which fills in the area of the lateral stripes.

In general coloration *T. s. tetrataenia* and *T. o. elegans* are very similar, as both have black dorsal ground color, bright yellow dorsal stripe, and pale yellow lateral stripes, but *tetrataenia* has red marks along the sides which in *elegans* are lacking and are replaced by yellow lateral flecks.

Along the coast of Humboldt and Mendocino counties in California, there is again parallelism in color pattern, in this instance between *T. s. infernalis* and *T. o. atratus*. Both have bright yellow dorsal stripes and red marks on the sides which tend to blend into the brownish gray ground color. They are thus difficult to distinguish unless actually caught and examined. Specimens of both species were found by me under similar habitat conditions in this region, and their ground colors seemed to match the background of dry grass against which they were usually seen.

Although the species *sirtalis* and *ordinoides* are similar in color pattern in certain limited areas, there is no general parallelism in trends of color pattern throughout their ranges.

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Winter Habits of the Red-Eyed Towhee in Eastern Kentucky

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During the fall and winter of 1937-38 the writer made an investigation into the winter habits of the Red-eyed Towhee (*Pipilo erythrophthalmus erythrophthalmus* Linnaeus) in the vicinity of Morehead, Rowan County, Kentucky. Very little material has been published on the winter habits of the towhee, and it is hoped that the following data will be of interest.

Habitat

The towhee in Eastern Kentucky inhabits in winter an area that contains two distinct ecologic units. In every instance observed by the writer, the area inhabited by the birds included one unit that was primarily woodland, and another that was primarily herbaceous. It is evident that the towhee is a bird of the forest border.

Wilson (1810) wrote of the towhee, "he is fond of thickets with a southern exposure, near streams of water, and where there are plenty of dry leaves."

In accordance with this observation, the writer has noted that six out of nine flocks observed were most often found along the edges of comparatively large streams. The three other flocks frequented streams which were often dry. Apparently, it is not the presence of water that attracts the birds as much as it is the abundant food and cover generally present along the stream.

The size of the territory ranged over by the winter flocks of towhees is naturally very variable. One flock, consisting of twenty-seven birds, ranged over an area approximately one hundred and fifty yards wide and three hundred yards long. Another flock, numbering twenty birds, was known to range over an area about three hundred yards wide and five hundred yards long. In the latter area the food and cover plants were much less dense than in the former. There are a number of factors that enter into the determination of the size of the area ranged over by any given flock of towhees. Apparently four of the most obvious of these factors are the size of the flock, the amount of cover present, the amount and quality of food present, and the climatic conditions.

Flock Size

There is a difference of opinion in the literature as to whether or not towhees associate in flocks. Wilson (1810) and Heil (1909) are agreed that towhees are not gregarious. Forbush (1929 wrote, "the family keeps together for a time, but seldom, even in migration, is anything like a close flock formed." Audubon (1856) stated that towhees "never associate in flocks."

However, Roper (1913) reported "a flock of fifteen or twenty towhees."

During the course of this investigation, nine rather loosely organized flocks of towhees were kept under observation. Other flocks were noted, chiefly in the vicinity of Carter Caves, Carter County, Kentucky. The average number of birds observed in the nine flocks was found to be seventeen, the numbers ranging from eight to twenty-seven birds. In regard to the sex ratio in the flocks, there was found to be a vast preponderance of males, the females totalling only 23.7 percent of the flocks. In summer, the ratio became much more nearly 50-50. This discrepancy in the winter flocks is probably due to the females migrating farther south.

Associates

In nearly every flock of towhees observed, Eastern Cardinals *(Richmondena c. cardinalis)* were present in numbers varying from one to eighteen. Slate-colored Juncos *(Junco h. hyemalis)*, Song Sparrows *(Melospiza melodia)*, White-throated Sparrows *(Zonotricia albicollis)*, and Field Sparrows *(Spizella p. pusilla)* usually were present in variable numbers. Tufted Titmice *(Baeolopus bicolor)*, Winter Wrens *(Nannus h. hiemalis)*, and Carolina Chickadees *(Penthestes c. carolinensis)*, were very often intermingled with the flocks. On one occasion House Sparrows *(Passer domesticus)*, were noted associating with the towhees, and on another occasion, Eastern Hermit Thrushes *(Hylocichla guttata faxoni)*, were seen in the flock.

Calls

Roberts (1932) states that "the two most common notes of the towhee . . . *towhee* and *chewink* — are distinctly given and unmistakable. . . . There are various other call notes, among them a simple "wee," a sparrow-like "sst," and, when disturbed around the nest, both sexes are "vigorous scolders." The writer has never been able to distinguish the two notes "towhee" and "chewink." However, it must be kept in mind that the call "towhee" is subject to considerable variation. One of the most commonly heard variations of this call was a distinct "oree." Probably the call "towhee" and its variations were used to make or maintain contact with the other members of the flock. At numerous times this call was heard uttered in a very low, ventriloquistic manner, causing the bird to be very difficult to locate. In every instance, this call came from on or near the ground in the concealment of a thicket. The simple "wee" noted by Roberts (1932) was heard on numerous occasions and apparently functions as an alarm note. Various towhees have been heard to utter a buzzing sound of three notes, the first and third notes identical, and the second note slightly higher. This is possibly the "sst" noted by Roberts (1932).

Galloway (1897), Dawson (1903), and Allard (1928) have each written of a rather uncommon and little known song of the towhee. This song was

noted by the writer on numerous occasions during the winter. It was a low, elusive bit of generally complex melody consisting of no definite number of notes, but varying from a simple trill to a very complex melody lasting several seconds. The song was almost always concluded by the call "towhee," and was often interrupted by that call. In every instance, the bird uttering the song was on or very near the ground in the concealment of a thick bush or pile of brush.

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Microdalyellia gilesi -- n. sp., a New Turbellarian Worm from Mountain Lake, Virginia

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In the summer of 1934 a number of specimens of a Turbellarian worm belonging to the genus Microdalyellia were encountered in collections made by the senior author from the type locality, a horse trough back of the old Mountain Lake hotel. During the next five years hundreds of similar individuals were obtained not only from Mountain Lake but also from various points in the Blue Ridge Mountains of Virginia. The worm proved to be a new species of this genus and we have given it the specific name *gilesi* after Giles County, Virginia, in which it was first found.

Our description of *Microdalyellia gilesi* is based on a study of more than a hundred individuals. Living animals were observed in the normal state as well as under pressure. For preserved specimens Allen's B-15, Zenker's, Bouin's and Beauchamp's fluids were used for fixation; Delafield's and Heidenhain's hematoxylin for staining; and sections were cut at 6 to 8 micra. Numerous acetocarmine smears were made and these proved of value not only in studying the chromosomes but also in determining the structure of the cuticular apparatus of the male reproductive system. This apparatus was also studied by dissolving away the tissues of the body with KOH. All measurements given in this paper are an average obtained from observations on at least 15 mature individuals.

Microdalyellia gilesi is larger than most species of this genus, being 2.0 to 3.5 mm. in length. In the normal (not compressed) individual the diameter is not more than one third of the length. The anterior end is truncated and the diameter of the body increases posteriorly until the maximum is reached at the level of the pharynx. It then tapers gradually to the bluntly pointed caudal extremity. The heavy pigmentation so frequently present in members of this genus is much reduced in this species. There is enough pigment present in cells of the parenchyma to give the body a light reddish brown color, yet it is not so dense as to prevent observation of the internal organs of the living animal. Cilia (Fig. 1, *c*) occur overall and their length is 11.2 micra. Sensitive hairs (Fig. 1, *sh*) are found at either end of the body, those at the anterior end, with a length of 17.8 micra being only about half as long as those at the posterior end whose length is 33 micra. Small clusters of rhabdites are scattered generally beneath the body surface. They vary in length from 4 to 7 micra with an average of about 5. There are seldom more than 8 to 10 rhabdites in a group. The two kidney shaped eyes (Fig. 1, *e*) have a brownish red raspberry-like color and are slightly closer to the sides of the body than to each other. They are located at the antero-lateral margins of the bilobed ganglion (Fig. 1, *g*).

The mouth (Fig. 1, *m*) is subterminal in position and opens into the pharyngeal sheath, (Fig. 1-*ppo*). The large cask-shaped pharynx (Fig. 1, *ph*) extends through about two sevenths of the body length and its base is surrounded by a ring of well developed glands (Fig. 1, *pg*) opening into the oesophagus and corresponding to the so called "salivary" glands which are found in many species of this genus. There is, however, no sign of glistening bodies within the gland cells such as are described by Graff (1911 and 1913) for *M. rossi*, a closely related species. Powerful retractor muscles (Fig. 1, *pm*) have their origin in the body wall and their insertion on the pharynx. A very short oesophagus concealed by the pharyngeal glands in the living animal, connects the pharynx with the rounded sac-like enteron (Fig. 1, *en*).

Judging by the contents of the enteron and by actual observations on feeding habits, *Microdalyellia gilesi* must be largely carnivorous. Cannibalism is prevalent and small animals were frequently observed within the enteron of larger animals. This species may also be parasitized by a nematode worm which is found in the enteron of infected specimens.

The genital pore (Fig. 1, *cgp*) lies in the midventral line at the beginning of the last body fourth and is surrounded by well developed sphincter muscles which regulate the size of the opening. The epithelium in this immediate vicinity lacks rhabdites although numerous glands are present around the pore, and around the genital atrium into which the pore opens. This latter is a comparatively small chamber with which the various portions of both male and female systems are connected.

The female reproductive system consists of the same fundamental parts which are present in most species of this genus. The bursa copulatrix (Fig. 1, *bc*) is shaped somewhat like a chemical retort and has muscular walls. The narrow proximal neck portion, extending dorso-anteriorly from the genital atrium has very heavy bands of circular muscles in its walls, while the expanded distal portion which forms an enlarged blind sac has much thinner walls in which there are no conspicuous muscular thickenings, although muscle fibers are present. The shape of this portion is not so constant as that of the much thicker walled neck. Within the bursa lie several (usually four) gourd-shaped structures. These are spermatophores, and the small number (seldom exceeding six) together with their characteristic shape and large size are good diagnostic characters for this species.

The uterus (Fig. 1, *ut*) is a sac with thin elastic walls, extending in a posterior direction from the genital atrium. Its size depends on the number and size of the eggs which it contains. Normally there is only one egg (Fig. 1, *eg*) present but it is not unusual to find more and occasionally as many as four or five eggs have been observed within the uterus of a single animal. The eggs are covered with a dark yellowish brown shell and are operculate as may be seen when they are soaked in NaOH. They are ellipsoidal and reach a maximum diameter of 150 to 200 micra. Well developed sphincter muscles control the size of the normally narrow passageway between the uterus and the genital atrium.

There is a single compact ovary (Fig. 1, *ov*) lying antero-lateral to the genital atrium with which it is conneected by a short oviduct (Fig. 1, *ovd*). The oviduct has an expanded portion which frequently contains spermatozoa and must, therefore, serve as a receptaculum seminis (Fig. 1, *rs*). The paired vitellaria (Fig. 1, *vit*) are dorsal to the testes and extend anteriorly to about the level of the posterior end of the pharynx. They are lobed throughout their extent, the lobes being relatively thick and close together as described by Graff (1911) for *M. sillimani* rather than long, fingerlike, and relatively widely separated as in *M. rossi*. The vitellaria of the two sides unite to form a common duct which joins the uterus and oviduct at their junction near the genital atrium.

The paired testes (Fig. 1, *te*) lie laterally in the body and are compact elongated organs. They extend into the anterior half of the body ventral to the vitellaria, thereby, placing this species in the subgenus *Microdalyellia*. Extending posteriorly from each testis is a thin walled tube of variable diameter, the vas deferens (Fig. 1, *vd*). The left vas deferens crosses ventrally beneath the vesicula seminalis to fuse with its fellow from the right side before penetrating the distal median ventral surface of the vesicula seminalis. The vesicula seminalis (Fig. 1, *vs*) is nearly spherical in shape and has thick muscular walls. The vesicula granulorum (Fig. 1, *vg*) which joins its distal end is, however, more pear-shaped with the narrowed end of the pear continued as the ductus ejaculatorius and finally terminating in the male genital canal. The granular glands are well developed. Many of them lie outside of the vesicula granulorum and empty their products into this organ by means of long ducts.

Within the male genital canal lies the cuticular apparatus (Fig. 3). This is of the *M. rossi* type. There are two main stalks (Fig. 3, *sta*) connected by a cross piece from which arise four end projections, a median dorsal (Fig. 2, *mdb*), a median ventral (Fig. 3, *mvb*) and two lateral end pieces (Fig. 3, *ldb*). The lateral end pieces bear spines (Fig. 3, *spi*) but the numbers of spines is not constant. Exact measurements which were made on 28 of these organs disclose a wide range of variation not only in the size of the organ as a whole but also in the relative sizes of the different parts. The following figures, all of which refer to the length of the structures mentioned, indicate some of the variations: (1) the entire organ: maximum 230 micra, minimum 142 micra, average 180 micra; (2) the individual stalks: maximum 160 micra, minimum 90 micra, average 125 micra; (3) lateral endpieces: maximum 80 micra, minimum 35 micra, average 60 micra; (4) midventral process: maximum 82 micra, minimum 41 micra, average 64 micra; (5) mid-dorsal process: maximum 60 micra, minimum 35 micra, average 51 micra. The variation in the number of spines on the lateral end pieces was also noteworthy. On the right lateral endpiece the number varied from 5 to 10 with an average of 7, while on the left lateral endpiece there was a larger number and at the same time less variation. The maximum here was 14, the minimum 11 and the average 12.

The following generalizations may be made: The stalks are at least twice as long as the end pieces.* The left lateral end piece is usually at least slightly longer than the right. The mid-ventral process is usually slightly longer than the end pieces, while the mid-dorsal process is shorter than the end pieces. A small terminal spine (Fig. 3, *ts*) may or may not be present on the left lateral end piece. All of the spines have their origin from the ventral surfaces of the end pieces.

The mature sperm cell (Fig. 4a) is threadlike, up to 60 micra in length and has two flagella (Fig. 4, *fl*) attached near its anterior end. While sometimes difficult to observe these may always be found after careful study. When the sperm are placed in water they swell instantly into a variety of shapes, some of which are shown in Fig. 4 (b, b′, b″). While many of these shapes seem to be constant there is no apparent gradation between them. The significance of this situation is unknown. Mature sperm for our study were taken from the bursa. The chromosome number in this species is n=2; 2n=4. The members of the two pairs are indistinguishable. Each chromosome is about three micra long and has a submedian centromere. Figure 5 represents an early telophase of a reduction division.

The paired end stems (Fig. 2, *es*) of the excretory system open ventrally by pores (Fig. 2, *prp*) located on either side of the body just anterior to the level of the gonopore. Each end stem is formed by the union of an anterior and a posterior main stem. The posterior main stem (Fig. 2, *pms*) begins in a small tubule coiling over the genital organs on the dorsal side near the level of the gonopore. This continues posteriorly to a point just beyond the posterior end of the uterus where it passes downward to the ventral side and redoubles on itself to run anteriorly and laterally almost to the nephridiopore. Just before reaching this opening, however, it bends dorsally again and extends anteromesially dorsal to the posterior end of the enteron. When it reaches a point near the median line and almost three fifths of the body length from the anterior end the posterior main stem turns sharply laterally and continues onward to join the anterior main stem (Fig. 2, *ams*). This latter is formed by the union of the anterior secondary stem (Fig. 2, *ass*) with the ventral secondary stem (Fig. 2, *vss*). The ventral secondary stem which lies entirely on the ventral side begins near the median line at about the level of the junction between pharynx and enteron. It passes posteriorly in a slightly lateral direction almost to the level of the excretory pore, where it makes a hairpin turn and continues anteriorly to join the anterior secondary stem. This latter begins near the median dorsal line at about the level of the middle of the enteron. It passes anteriorly and laterally to the midpharynx level and then bends mesially so as to run just mesial to the eye. This is the ascending limb (Fig. 2, *dpb*) and it makes an S curve before terminating its anterior course in a hairpin turn. The descending limb of the hairpin lies slightly mesial and parallel to the ascending limb until it reaches the anterior border of the pharynx where it crosses over the ascending limb and continues latero-posterior-

* One exception was found in the 28 measured and in this specimen the stalks (which may not be complete) were only a few micra short of the required length.

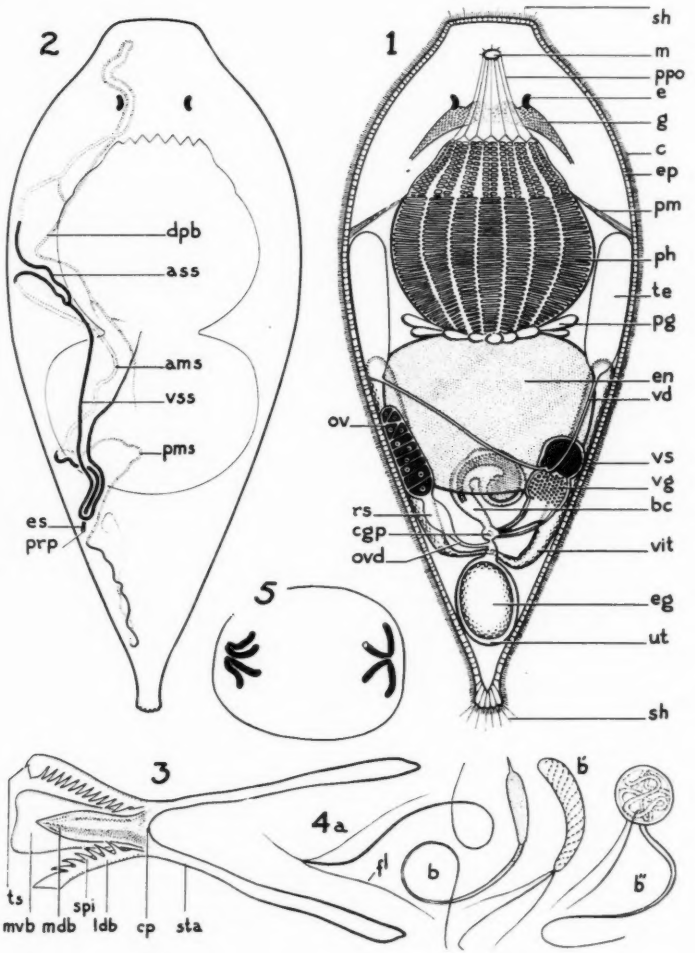
ly. There is a cross connection between the ascending and descending limbs of the anterior secondary stem at about the level of the first third of the pharynx. At the midpharynx level the anterior secondary stem turns downward to the ventral side and bends mesially so as to meet the ventral secondary stem on the ventral side near the postero-lateral margin of the pharynx. The junction of these two large branches forms the anterior main stem which extends antero-laterally for a short distance before turning abruptly upward to the dorsal side and reversing its direction so as to run postero-mesially on the dorsal side. Slightly posterior to the junction between pharynx and enteron the anterior main stem bends laterally again. Near the postero-lateral border of the enteron it is joined by the posterior main stem and this union marks the beginning of the end stem. The end stem turns ventrally, follows the posterior boundary of the enteron for a short distance and then bends posteriorly and extends postero-laterally to the excretory pore. Numerous smaller side branches empty into all of the main channels except the end stems. All of the tubules pursue a somewhat meandering course through the body, seldom following a straight path for any appreciable distance. The protonephridial tubules reach a maximum diameter of 11 to 12 micra. The flagella of the flame cells reach the unusual length of 22 micra.

Summary

This paper describes a new species of *Microdalyellia* from Virginia. Ruebush (1937) recognizes 16 valid species of this genus from America. The present form brings the total to 17. *M. gilesi* belongs to the subgenus *Microdalyellia* as do a number of the other American *Microdalyellia* but it shows a number of unique features which warrant ranking it as a distinct species. A study of more than one hundred specimens has revealed that it may be clearly differentiated from other species of the genus on the basis of: (1) anatomical differences in the cuticular stilette; (2) number, size and shape of the spermato-

ABBREVIATIONS USED

ams—anterior main stem
ass—anterior secondary stem
bc—bursa copulatrix
c—cilia
cgp—common genital pore
cp—cross piece
dpb—dorsal pharyngeal branch
e—eye
eg—egg
en—enteron
ep—epidermis
ep—epidermis
es—end stem
fl—flagella
g—ganglion
ldb—lateral distal branch
m—mouth
mdb—median dorsal branch
mvb—median ventral branch
ov—ovary
ovd—oviduct
pg—pharyngeal glands
ph—pharynx
pm—retractor muscle of pharynx
pms—posterior main stem
ppo—pharyngeal pocket
prp—protonephridial pore
rs—receptaculum seminis
sh—sensory hair
spi—spine
sta—stalk
te—testis
ts—terminal spine
ut—uterus
vd—vas deferens
vg—vesicula granulorum
vit—vitellaria
vs—vesicula seminalis
vss—ventral secondary stem



Figs. 1-5.—*Microdalyellia gilesi:* 1, Ventral view of the gross anatomy (×35); 2, protonephridial system (×35); 3, cuticular apparatus of the male reproductive system (×350); 4a, mature normal sperm (×1000); 4b, three sperm swelled by contact with water (×1000); 5, chromosomes in early telophase of reduction division (×3650).

phores in the bursa; (3) shape and structure of the bursa itself; (4) size, shape and pigmentation of entire animal; (5) various unique features of both male and female reproductive systems; (6) features of the excretory system which differ from this system as described in other species; (7) various minor points which serve to distinguish this species from others closest to it in general structure, if not from all other species of the genus.

Species Diagnosis

Microdalyellia gilesi n. sp.

Length 2.0 to 3.5 mm. Diameter $^1/_3$ length; spindle shaped; cilia overall; sensory hairs terminal; rhabdites small in clusters; eyes, one pair, brownish red, kidney-shaped, closer to the sides of the body than to each other; mouth subterminal; pharynx large with ring of well developed "salivary" glands at its base; genital pore in mid-ventral line at beginning of last body fourth with well developed sphincter muscles and glands; well developed retort-shaped muscular bursa containing four (sometimes 3 to 6) characteristic large gourd-shaped spermatophores; uterus large with one (not infrequently several) large operculate eggs; ovary single; compact; enlarged proximal portion of oviduct serving as receptaculum seminis; vitellaria paired, dorsal to testes, and with thick short lobes; united portion of vitelloduct enters junction between uterus and oviduct; testes paired, compact, ventral to vitellaria, and extending into anterior body half; vasa deferentia of two sides unite before entering globular vesicula seminalis; granular glands mostly outside of pear-shaped vesicula granulorum; well developed muscular male genital canal; cuticular apparatus of male copulatory organ of *M. rossi* type with two stalks joined by a cross piece from which median dorsal, median ventral and lateral end pieces originate; lateral end pieces armed, 11-14 spines on left, 5-10 on right; sperm cells long thread like with two flagella; excretory system paired throughout, excretory pores ventral near level of gonopore; one end stem on either side formed by the union of an anterior and a posterior main stem, anterior end stem in turn formed by union of anterior secondary stem with ventral secondary stem. Habitat: freshwater. Distribution: Virginia: Mountain Lake, Swift Run Gap, Afton and other points in the Blue Ridge Mountains. Cotypes: Whole mount, transverse and longitudinal sections on slides, U.S.N.M. No. 20548.

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Twenty Years' Statistical Studies of Marine Plankton Dinoflagellates of Southern California*

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Introduction

Adrift in Southern California seas two distinctly different types of microscopic organisms possessing powers of photosynthesis are represented continuously and are able to reach notable abundance with considerable frequency. These are the diatoms and the dinoflagellates. On account of their greater abundance in most of the Scripps Institution collections the diatoms are discussed more extensively in other papers (Allen 1936 and earlier). Discussion in this paper is limited to the dinoflagellates, and it deals mainly with representatives of only a few of the major groups, the exact designations and limitations of the groups depending on what authority is consulted for classification. It is not even possible to find full agreement as to their being plants, although recent botanical books (e.g. Fritsch 1933) give good arguments for considering all of them plants.

For present purposes it is unnecessary to give particular attention to classification beyond saying that the organisms under consideration are microscopic, biflagellated, unicellular plants adrift in the sea, mostly included in seven genera; i.e. *Peridinium, Ceratium, Goniaulax, Prorocentrum, Dinophysis, Noctiluca,* and *Gymnodinium*. The genus *Gymnodinium* is used here as a catchall for the numerous unarmored forms appearing in the collections. A few other genera are represented in negligible numbers in Scripps Institution series of catches.

It is probable that all specimens included in Scripps Institution records are photosynthetic in activity, and therefore eligible to consideration as components of "ocean pasturage." On the other hand, there is evidence to suggest that their nutritive values, or characters, are hidden at times by characters injurious to animals (cf. p. 13) which are developed or exhibited when dinoflagellates appear in dense populations (Allen 1921a, 1921b, 1933, and other papers).

Phytoplankton investigations of 1917 (first year) and 1918 were unsatisfactory for a number of reasons: First, there were no standard stations at which permanent series of continuing and frequent observations could be made in order to establish and improve a reliable basis of understanding of conditions normal to the region. Second, it was impossible to standardize the operation of tow nets or to avoid the numerous widely ranging errors (Allen 1921a, p. 540) due to progressive clogging of the meshes, to irregular movements in

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hauling, and to mixing of populations not actually associated in certain spots or levels traversed. Third, it was impossible to know what volume of water yielded any particular catch, much more or much less water being filtered by any particular tow than was filtered by some others of the same distance and duration. Fourth, tow nets demanded great skill in hauling and favorable conditions for handling. Fifth, the cost of equipment and the loss of time involved in using tow nets for extended series of phytoplankton collections was too great.

Therefore, when phytoplankton investigation was advanced to the status of a full time activity of the Scripps Institution in 1919, improvements of methods and procedures received immediate attention and careful study. As a result, the measured water method was adopted as standard (Allen 1921b, 1936). Until 1929 the routine of using this method by the Scripps Institution was as follows: A known volume of water (five to twenty-five liters) was dipped from the sea and filtered through a small conical net of No. 25 bolting silk (80 meshes per centimeter or 200 meshes per inch, linear in new material). Sometimes the water was measured before pouring through the filter, sometimes as it came from the filter. The Kofoid (1911) closing bottle was used for getting samples below the surface in a few series. Later, the smaller and lighter Allen (1927) closing bottle was used for subsurface sampling. For catching the larger, armored dinoflagellates, this filtration method was probably as dependable as any in addition to being easier and faster in routine operation. For smaller forms, it was less satisfactory; the losses of *Prorocentrum* and others through the meshes of the filter creating a notable uncertainty. Still, most of the catches were good enough to show the main tendencies in occurrence and distribution of the dinoflagellates as a group.

Partly for convenience but mainly for better catching of smaller forms a concentration (settling) method of collecting was adopted in 1930 for the Scripps Institution pier in place of the filtration method which had been used through the first decade. One liter of water was placed in a glass cylinder with enough formaldehyde (five to ten milliliters) to kill the organisms for removal after twenty-four hours by successive decanting and pipetting.

Laboratory treatment of catches consisted in the routine of counting the organisms in a measured fraction of a catch, in one milliliter of water in a Sedgwick-Rafter counting cell, under a compound microscope. For thin populations in clean water the fraction was usually one tenth of the Sedgwick-Rafter sample. For dense populations or heavily silted catches it might be as little as one hundredth for particular species in a much diluted sample, representing no more than five thousandth of a liter of untreated water in a few cases. The magnification used for counting was usually about one hundred diameters. From the count records the numbers in the catch were estimated, and from these estimates calculations were made of the numbers per liter in the water sampled. In the later years separate calculations were made for those specimens in good condition (alive or viable when caught) and for those in bad condition. The series of records thus obtained were used for finding relative densities of dinoflagellate populations in periods of days, weeks, lunar months, seasons, and years. They were used also for comparing occurrences

of entire dinoflagellate populations or of selected species under natural conditions in one or several localities.

The largest number of catches (about 6,500) was obtained from the water at the seaward end of the pier of the Scripps Institution of Oceanography, on La Jolla Bay, a little north of San Diego Bay on the Gulf of Santa Catalina (see map Fig. 1.) Almost as many were taken from a similar position inshore

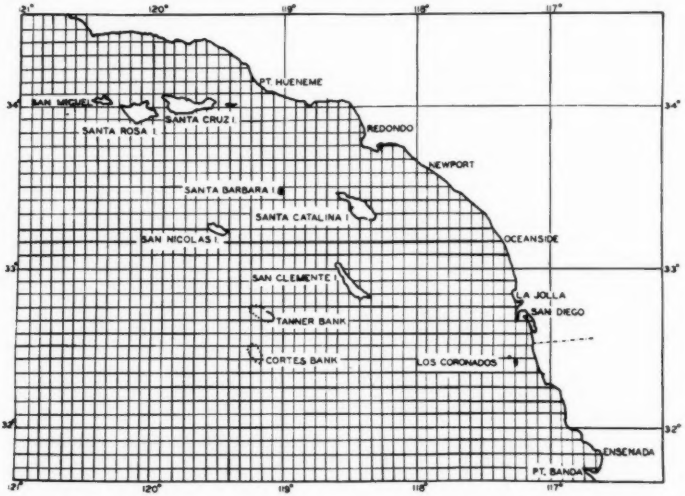

Fig. 1. Map of coastal waters of Southern California to show location of standard stations La Jolla and Pt. Hueneme in region of greatest activity in oceanographic research of Scripps Institution.

at Pt. Hueneme, more than one hundred miles northwestward. About 2,000 catches were made at other inshore stations between these, and some thousands were made at offshore positions on different trips by boat. In addition, a number of series of collections from the surface level were made in localities more or less distant from California. Altogether, more than twenty-five thousand catches have been examined at the time of this writing in 1940.

Ocean Habitats

A considerable success in understanding and controlling the life of land plants has been attained without very prominent attention to the phenomena of stratification in the various habitats. Such neglect of important conditions in space relationships may be due in part to the knowledge of investigators that many kinds of conditions in levels both above and below the soil surface may differ or change suddenly and extremely, and that in some cases these changes occur often.

But the student of plant life in the sea who seeks to understand the condi-

tions of its existence cannot escape a continuing emphasis upon the importance of distance below the surface, whether stratification be recognizable or not. There, he finds that vertical zonation is rarely less important than horizontal zonation, and that it is more important in certain particular invetsigations. At first, he may feel much relieved by the thought that the pelagic plants are all continuously and completely resident in the one medium, sea water, and that they are so small that their entire bodies can be engulfed in any stratum of observable thickness. He may feel still more relieved when he finds that the sea differs from the land in the relatively high uniformity of its chemical composition, a uniformity so great that the ordinary differences are expressed in thousandths or other small fractions of units. But, he may be greatly disturbed, or confused, when he realizes that these microscopic marine plants may be readily transported from stratum to stratum, or that they may be carried into a turbulent spot in which general mixing of zonal residents, components and inclusions occurs. In fact, if he be requested to characterize an ocean habitat he may be unable to decide whether the locality showing an observed population, or the mass of water carrying it, or the series of localities concerned in its production shall be designated.

On the land it is possible to select individual plants, or groups of plants, for study in relation to a specific place of residence. In study of the drifting populations of the sea it is necessary to select a place of observation and to use whatever plants are found in it from time to time. If a locality be selected for study on land, one expects to find its population fairly stable over a considerable period of time. In the sea, a dense population of a particular kind may appear in an observed locality for a few hours or days, not to be strongly represented again for years. A plant or a population may appear at a level at which it is not usually found, or it may be found most often at a certain level in one locality and at a different level in another. Ordinarily, the constant movements of the plants in one direction or another add enormously to the difficulty of conducting researches and of understanding the results of researches.

When discussing the habitat relationships of phytoplankton, the fact that populations are themselves significant features of their own habitats should not be neglected. Not only are they continuously modifying their immediate surroundings but they are also modifying themselves. In the ocean, both types of changes are likely to occur with remarkable speed and abruptness, e.g. when an increasing phytoplankton population modifies its activities as nutrients decrease, while changing the forms of these nutrients in such ways as to accelerate or retard solution, decomposition, or formation anew of numerous sea water inclusions.

In consideration of the foregoing, and of a number of other points which might be mentioned, it seems that ocean habitats in the sense of places of residence of particular phytoplankton populations are as varying and as varied as the populations which they support. Not only does one locality differ from some other at any given time, but it also differs within itself from time to time. However, these differences in respect to space, time, and population history tend to show recognizable groupings according to geographic relation-

ships. Most clearly exhibited is the fact that shallow depths like those of La Jolla Bay entail conditions of temperature, complex water movements in all directions, and inclusions of materials from land not to be found at any time in mid ocean. Still, it may be difficult to determine the relationships of phytoplankton populations to one region as distinguished from the other. Perhaps one may say with considerable assurance that the high seas directly off shore from La Jolla Bay have no influence upon it, or it upon them, the general circulation of the Gulf of Santa Catalina being too strongly effective upon the water masses between them. On the other hand, it is impossible to believe that production of phytoplankton in La Jolla Bay would be the same as now if the deep ocean were not out there.

When the measured water method of collecting was first adopted at the Scripps Institution of Oceanography in 1919, so little was known about the distribution of phytoplankton in relation to locality differences of habitat that no effort was made to identify habitat peculiarities at the Institution pier. The sufficient reason for collecting there was proximity to the home laboratory with its most favorable opportunities for convenience in operation and continuity in observation. As soon as daily collections showed the probability that samples of phytoplankton obtained at this inshore station were fairly representative of the region, plans were made to begin daily series of collections at one or more stations in other localities in order to compare the information obtained from them with that being accumulated at the home station. Consequently, in February 1920, daily (except Sunday) collections were begun at Pt. Hueneme, near Oxnard, California. The immediate reasons for selecting this station were: that it was more than one hundred miles distant from the home station; that it was already being used by the Scripps Institution for hydrographic observations; that a dependable collector resided there; and that its location north of the Gulf of Santa Catalina suggested the presence of recognizable habitat differences.

Even in 1940, positive knowledge covering the details of significant habitat differences at these two places is lacking. The most that can be said is that certain gross features characterizing them seem to be observable. The existence of lower temperatures of sea water month by month (Fig. 2) at Pt. Hueneme is clear. So, also, is the slightly longer duration of winter influences. Greater turbulence at this station at the eastern end of Santa Barbara Channel is to be expected, and there is evidence that it exists. Also the relative proximity to fairly large islands and to a more considerable land drainage suggests the probability that significant differences do exist there. But, aside from these imperfectly defined features, there is little known about monthly, seasonal, and annual, or cyclical differences in the ocean in the two localities.

Concerning the home station, it may be noted that the Scripps Institution pier, one thousand feet in length, is located on the eastern shore of La Jolla Bay, near the northern end of a mile-long, gently sloping beach, and at the southern end of a four mile series of cliffs, based on moderately hard sedimentary rocks and faced with varying aspects of conglomerates and of silty shales of differing degrees of hardness. The nearest stream of appreciable size enters the ocean at the northern end of this series of cliffs, except in the dry

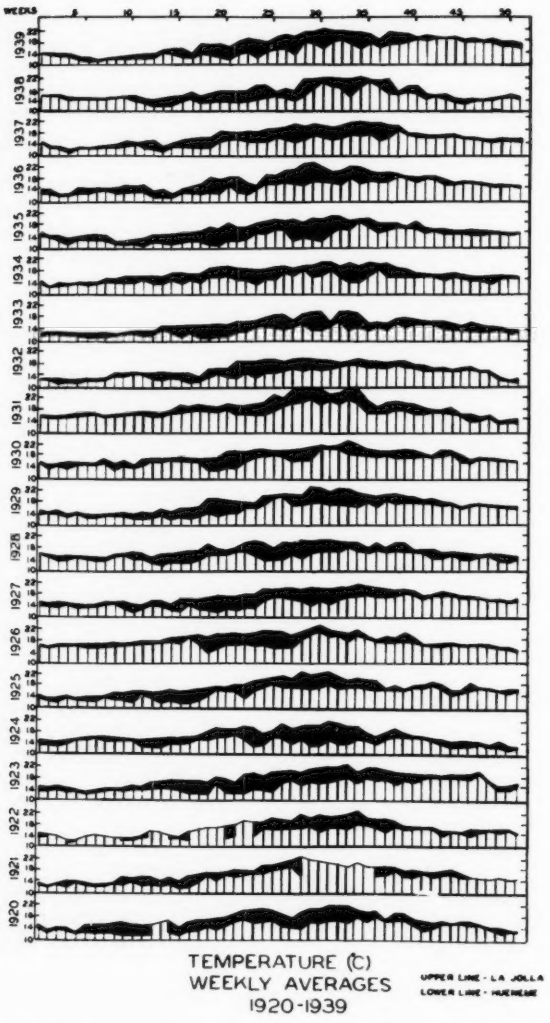

Fig. 2. Graphic representation of yearly temperature progressions; shaded between lines to stress station differences. Upper margin La Jolla. Lower margin Pt. Hueneme.

season. The beach occupies about two-thirds of the base of a triangle with its apex about a mile seaward from the end of the pier, the southwestern side consisting of a submerged canyon deepening to a thousand feet or more at the apex where it is joined by a similar canyon of nearly westerly trend which extends from shore about a half mile north of the pier. On the triangle the slope increases very moderately to seaward until much steeper contours occur at about two thousand feet from shore, the depth at the end of the pier being less than twenty-five feet at ordinary high tides. The pier extends a little north of west. In this position it is exposed directly to the open ocean, the nearest obstruction off shore being San Clemente Island at a distance of more than sixty miles.

As recently as 1919 the beach terminated in a rocky shore a few yards north of the pier. In those days it was sometimes denuded of sand throughout half its length in winter seasons when the underlying rock strata became bare where not covered with enormous deposits of "cobble stones" four inches or more in diameter. At other times the sand deposits of the beach might be increased by depths of two or three feet temporarily. In more recent years, these seasonal changes have been less evident and the beach has been extended northward over the rocky foreshore until it has become difficult to find good tide-pool collecting grounds, except at lowest tides, within a short distance of the pier. Such changes are probably incidental to the cutting back of the shore cliffs many yards by surf erosion (Shepard and LaFond 1940). Whatever the causes of changes in the beach levels and the like, these seasonal changes indicate that there must be marked disturbance in the waters of La Jolla Bay at times. The little evidence available concerning water movements outside of the limits of the small bay suggests that no prominent turbulence exists there, although the bottom contours may cause a certain amount of mixing of currents.

In general, therefore, it appears that oceanic waters may come into La Jolla Bay without being greatly influenced by conditions peculiar to the immediately surrounding territory. If this be true, one finds it impossible to suppose that the phytoplankton collected at the Scripps Institution pier is necessarily a product of La Jolla Bay or a resultant of the environmental conditions found there. In a period of long continued calm weather, perhaps the Bay does have a high degree of influence. In a whole year of very mild weather the local influence may be continuously notable, but in most years there must be long periods in which the local influence is relatively negligible in determining the condition of the populations there. Doubtless, many of the striking peculiarities of occurrence and abundance in different seasons and years are due to differences in degrees of prominence of local influences at the different periods. The only reliable conclusion available seems to be that La Jolla Bay may or may not exert notable influence upon the populations sampled within its limits, depending on the extent to which water movements, or lack of movements, permit its conditions to operate before the population shifts to another locality or disappears.

Why, then, do the phytoplankton populations of the Bay differ from

those at any particular locality of similar extent off shore? The evidence to support a dependable or comprehensive answer to this question does not exist. We must be content with certain inferences drawn from our limited knowledge of occurrences of populations and of selected features of the habitats so far sampled. Populations observed show that surface samples at the Scripps Institution pier and at considerable distances offshore may be closely similar, although recognizable differences are more likely to be found. Inasmuch as the shallow depth of water at the pier is sufficient alone to constitute a fundamental difference from any off shore habitat, it is surely true that the presence of similar populations in places more or less distant from each other is not a dependable indication that habitat conditions are also similar to a like degree. Three or more combinations or sequences of circumstances may be responsible primarily for this kind of irregularity. First, certain environmental features (e.g. abundance of phosphate) may be so prominent over a wide territory at some particular time that they cause production of particular populations in spite of local dissimilarities of other features recognizable but not detrimental within the limits of observation (e.g. high temperatures or unusual cloudiness). Second, the two populations inshore and offshore may have been drifted into their separate localities from a locality of common origin so recently that they appear to retain the earlier likenesses in recognizable form although already acquiring important differences. Third, a population developed in an area more or less off shore may be expanded into such an area as La Jolla Bay, adapting itself to environmental features of secondary, or tertiary, or more remote influences as the expansion progresses.

Importance of Plankton Dinoflagellates

Bigelow (1926), Bigelow and Leslie (1930), Kofoid and Swezy (1921), Lebour (1925), Fritsch (1935), West (1916), and other authorities ascribe great importance to the pelagic dinoflagellates, rating them second only to the plankton diatoms as contributors to the basic food supply in the open sea. However, Fritsch and some others are disposed to question the validity of an assumption that phytosynthetic activities of all planktonic vegetation are superior to those of all sedentary marine vegetation in providing food for animals inhabiting sea water. Still, in the absence of reliable data to prove superiority in food production for either pelagic or sedentary vegetation, it seems reasonable to give plankton dinoflagellates a high general rating, especially when it is recalled that they contribute largely to sustenance of sedentary animals as well as to those of free living habit. In addition, their influence on oxygenation and other chemical changes in sea water surely qualifies them for a prominent place when considering influences of organisms in the sea. Even though they be rated below pelagic diatoms in volume of constructive metabolism, as seems reasonable, they require attention because of the frequency of their occurrence in high abundance in many localities, and because of the possibility that peculiarities of their occurrence may serve to indicate the presence and distribution of chemical, physical, or biological conditions of localized water masses which might be overlooked otherwise.

Evidence of Productivity

Most of the literature which gives high rating to dinoflagellates as producers in the food chains, or food cycles, of the sea is barren of proof to support the assumption. As a matter of fact, direct proof of production of any designated quantity of nutritive material, or of its consumption or availability for consumption by animals is not obtainable from any large marine area over any considerable period of time. The most that can be done is to assemble evidence suggesting reasonable probabilities within closely limited boundaries and fair probabilities within more remote boundaries. It is believed that the Scripps Institution series of daily records of observatons for two inshore stations over a period of twenty years afford the best evidence concerning this point now existing anywhere in the world. Voluminous supplementary records from other Institution series add weight to this evidence.

Statistical studies of dinoflagellates in Southern California were begun on material obtained on boat cruises in 1917 at the same time that similar studies on plankton diatoms were begun (Allen 1921a). Although the methods of collecting by vertical and horizontal hauls of tow nets in 1917 and 1918 were so different from those used later that close comparison of numerical records is impossible, certain gross features of the records of that material collected by boat are still important. In particular, the occurrences of "red water" were remarkable; first, because they were more prominent than others observed by Scripps Institution investigators since that time, except for single occurrences in each of the years 1924, 1933, 1938 and 1939 (Allen 1928, 1933, 1938 and Institution records). Second because in September 1917 *Goniaulax polyedra* Stein made its last recorded appearance until 1938 as a cause of "red water" in the region covered by Scripps Institution investigations. However, these observations may be more interesting than significant because the "red water" of 1917 was found near San Pedro and Santa Barbara in localities rarely visited by Scripps Institution investigators in succeeding years. Still, the indication that *Goniaulax* waned in preminence after that year is not without importance, especially when it is noted that the "red water" of June 4, 1917, near La Jolla, was due mainly to *Prorocentrum micans* Ehr., the dinoflagellate most prominent numerically in the San Diego region up to March 1940.

Failure to find more than the four occurrences (1924, 1933, 1938 and 1939) of "red water" in the Gulf of Santa Catalina since 1917 has not been due to lack of interest in the phenomenon. Two reasons for interest are mentioned in the report on observations of 1917 (Allen 1921a, p. 544), "These two typical cases show not only that plankton swarms occur both inshore and offshore, but that they are to a very large extent exclusive against other organisms in their particular area, many of which, in fact, are killed." Another reason is that such strongly localized occurrences of concentrated plankton populations may indicate incident or related peculiarities of surrounding sea water worthy of special attention.

For support of the assumption, or assertion, that dinoflagellates rank very high as producers of ocean pasturage, most writers rely on reports of vast

assemblages of these organisms seen at certain times and places although the observations leading to the reports may be transitory. The fact that organisms may appear in such abundance as to constitute "soupy water" or "red water" as viewed from the surface of the sea is considered good evidence of productivity in general although the reported condition of the water may have been confined to a small locality, to a shallow surface layer, or to a few hours or days in time.

However, it is natural to reach first conclusions about productivity in nature from such gross observations, and the reputations for production or non-production of plants of many land areas have been established in just this way. It is only by subsequent studies of good continuity and extent in time and space that reasonable approximations to true ratings (larger or smaller than the originals) are reached. "Red water" (which always indicates high abundance of organisms) has been reported several times (Torrey, 1902, Kofoid, 1911, Allen, 1921, 1933, 1938) in the Gulf of Santa Catalina, and it has been seen at other times though not officially reported. Presumably, therefore, this region may be supposed to have contributed some support to the idea of high rank in productivity for dinoflagellates. On that account, it is necessary to inquire what relationship observed outbreaks of 'red water" have had to total production. In the twenty years of daily observations at La Jolla only four conspicuous examples of "red water" (in 1924, 1933, 1938, 1939) appeared. At another time a small area of "yellow water" was noticed in La Jolla Bay (Allen 1935), and on a few occasions streaks of reddish color appeared in the surf. Still, it is hardly permissible to say that "red water" abundance appeared in more than four years of twenty. Including the outbreaks reported by Torrey in 1902, by Kofoid in 1911, and by Allen in 1921, 1933, 1938, only six occurrences of such abundance are authentically recorded for Southern California in a period of more than thirty years. Nightingale (1937, p. 8) has listed eight occurrences of "red water" from California and Washington coasts since 1878. Obviously the sight of "red water" is important for its impressiveness rather than because of the reliability of its indication of general productiveness of dinoflagellates.

Less freqeuntly mentioned than "red water" as an indication of high abundance is "phosphorescence" (luminescence). At the Scripps Institution of Oceanography remarks have been heard often to the effect that dinoflagellates must be highly abundant because luminescence has been conspicuous in the surf or in the wake of fishes swimming near the pier. Luminescence is a much less reliable indication of high abundance than "red water" because of the fact that a little of it makes a great impression in darkness. Even when dinoflagellates and other luminescent organisms are present in relatively small numbers they give a startling display of light in a collecting bottle when formaldehyde is added to a fresh catch in darkness. Surely, we may conclude that luminescence is even less dependable than "red water" as an indication of productivity, local, regional, or general in space, or periodical in time.

Many years ago, students of plant occurrence and distribution on land learned the lesson that gross inspection (the transitory kind in particular) gave

no reliable information as to the productivity of plant populations in a designated locality. Even lumbermen dealing with large trees in forests apparently uniform resorted to detailed examination before making estimates upon which to base their plans of operation. If a plant census is necessary on land where visibility is good, it is more distinctly necessary in the sea where visibility is far inferior. Therefore, admitting that "red water" and other gross phenomena are insufficient as indications, it becomes necessary to base estimates of productivity on census taking fundamentally similar to that used for land plants.

One accustomed to work on land might suppose that a census taken at the surface of the sea would yield an acceptable basis of estimate of productivity for the sea, just as it does on land. However, a liter of water scooped from the surface even in "red water" might show so few organisms as to make him think that the larger abundance must be present a little below the surface. If furnished with proper equipment, he might find that abundance was greater at one meter depth than at the surface, but that it was still greater at depths of five or ten meters. That is to say, he would be forced to realize that no estimate of productivity can be complete unless it be based on census enumerations at all levels in which the organisms (at least the viable organisms) are found. The surface condition might be fairly representative, but there can be no escape from the strong probability that it might be poorly representative, or the possibility that it might be misrepresentative. Furthermore, the streakiness observed in "red water" at the surface indicates strongly that no one sample is closely representative of numbers present, or of density of population, at any selected level.

In the "red water" appearing at the Scripps Institution pier in 1924 (Allen 1928) catches taken at five meters depth were slightly larger for the second week than the regular surface catches. On the other hand, most catches taken at levels below the surface at off shore stations showed larger numbers of dinoflagellates at the surface than at other levels, the numbers usually decreasing at successive levels until few were found at one hundred meters or more. Of course the aggregate of numbers at all lower levels might be greater than the number at the surface, thus showing the surface level as not being truly representative of total numbers in the area or of conditions at other levels.

But, although the results of surface census taking are not completely dependable in estimating productivity of micro-organisms at any particular station or in any particular locality, they are still far more dependable than the results of gross inspection. This is true, not only because gross inspection is so narrowly limited in depth but because populations of large size may be present in numbers too small to cause observed discoloration. Furthermore, relatively thin populations producing over a long period might yield a higher aggregate than a dense population resident for a short period only.

Prior to the accumulation of daily catches recorded in numbers per liter through several years, it had been assumed (e.g. Kofoid and Swezy, 1921)

that dinoflagellates were regularly and frequently abundant in the Gulf of Santa Catalina. This assumption, founded mainly on numbers obtained by hauling tow nets through considerable distances (two hundred meters or more) was found to be erroneous so far as armored dinoflagellates are concerned. Catches taken by boat off shore, as well as those taken daily at the pier, rarely showed numbers greater than thousands per liter at any time of year. Indeed, numbers below a thousand per liter were taken more often than numbers above one hundred thousand. And, in the first ten years the totals of all catches for a single year reached a number of one million cells per liter

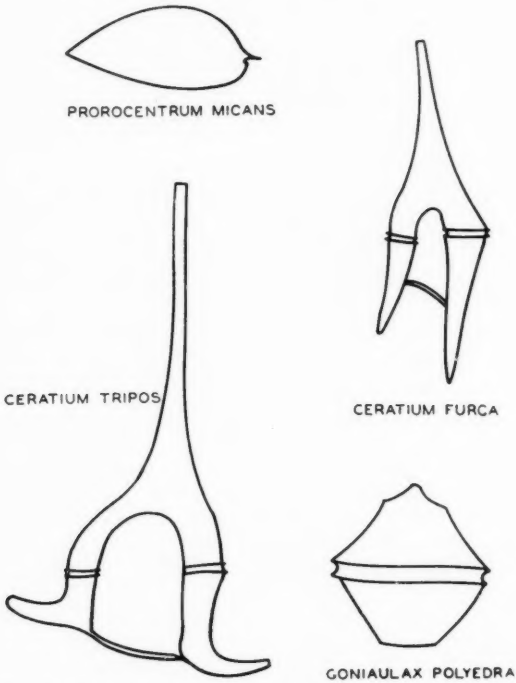

Fig. 3. Free hand sketches of four leading species from measurements of specimens in Scripps Institution collections

only twice at La Jolla and four times at Pt. Hueneme. To this implication that numbers of thousands per liter do not represent good production, an objection may be offered that pelagic, armored dinoflagellates are so much larger than diatom cells that smaller numbers may represent nutritive material equivalent to diatom populations showing numbers large enough to suggest

good production. Adequate data for comparison of nutritive values of individual cells of the two kinds of organisms in Nature do not exist. However, this deficiency is not so very important when considering Southern California material because *Prorocentrum micans* (Fig. 3) and other small dinoflagellates contribute most largely to total numbers of the group although the larger forms *Ceratium tripos* (Fig. 3) and *Ceratium furca* (Fig. 3) reach fairly high numbers occasionally and other species rarely. With all due allowance for larger sizes of armored dinoflagellates it seems fair to say that existing evidence does not indicate that their productivity is high in Southern California waters, although their larger size may suggest periods of influence relatively long. On the other hand, it is just as clear that their numbers have not been so low as to be entirely negligible throughout any year of twenty years.

Yearly Differences in Abundance

In dealing with large populations of creatures which are non-visible, both because of minute dimensions and because of physical limitations of the medium in which they are immersed, most observations and conclusions are necessarily more suggestive than positive in character. On the other hand, a good or high frequency of observations carried in regular series over a long period of time tends to offset this deficiency and to give much of the evidence thus accumulated a dependability fully as good as that relating to many populations easily visible. This is true particularly of phenomena such as those of differences in abundance from year to year, or between any two years.

Even a superficial inspection of the graph (Fig. 4) representing week totals per liter for the twenty years reveals that the distribution of numbers of dinoflagellates is different in successive years at both of the two stations observed. As a matter of fact, the magnitude of these differences would be vastly more distinct if space could be used to show the relative sizes of daily catches. Probably it would not be possible to assemble series of records concerning any population of organisms easily visible in Nature which would be more dependable than these as bases of comparison of year differences in gross features of occurrence. In fact, it is doubtful if any visible population in Nature is represented with observations of a frequency sufficient to make it equal to these records in reliability. Therefore, it may be assumed that these records not only suggest but support a fundamental fact i.e. that non-visible populations in the sea are changing in numbers throughout the year and from year to year. This fact is fundamental because it proves that adjustments and re-adjustments of populations are occurring constantly and perennially in Nature and because a correct understanding of marine biology can only be reached through an understanding of the causes and accompaniments of these shifting relationships.

But, although the duration, extent, and seasonal position of periods of abundance is always changing throughout the lapse of a year or of a series of years, there is a general pattern of change to be found in all years (Fig. 5). Furthermore, this general pattern of change is closely similar in at least one

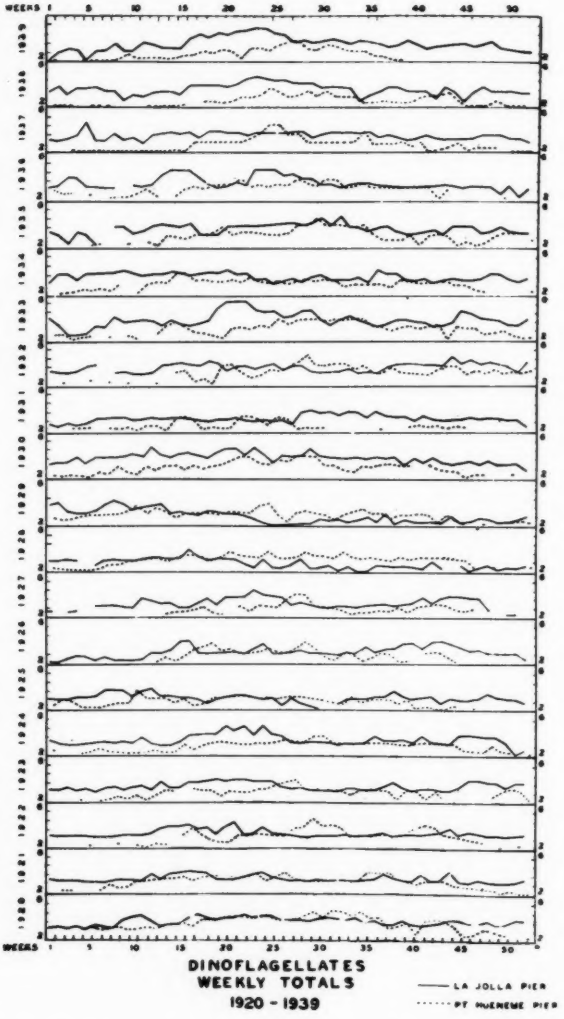

Fig. 4. Graphic representation of weekly successions of fluctuations in abundance of total armored dinoflagellates year by year. Solid line La Jolla. Broken line Pt. Hueneme.

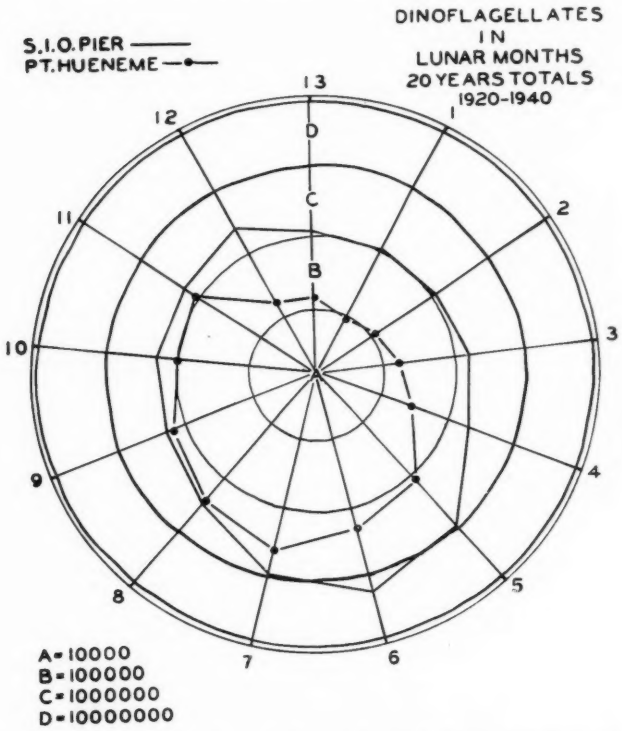

Fig. 5. Twenty year totals for each four week period of annual thirteen; to show trend toward higher abundance in summer in year pattern for abundance of armored dinoflagellates.

gross feature at both of the two standard collecting stations. This particular gross feature is the fact that the six months period halved by the summer solstice is more productive of dinoflagellates (usually much more productive) than the six months period halved by the winter solstice. At Pt. Hueneme, this condition approaches constancy in its annual repetition, but at La Jolla there are enough exceptions to render doubtful the tempting conclusion that productivity waxes and wanes regularly as the supplies of radiant energy wax and wane from the beginning toward the close of each calendar year. Prominent among these exceptions at La Jolla were four-week periods in November-December of 1923, 1924, 1933 and in October-November of 1932 which showed abundances similar to those in median parts of most years. The same is true of two-week periods at La Jolla in January of 1927 and 1936 and in February of 1930 and 1934 (Fig. 4). Still, these exceptions do not prove that

the waxing and waning of solar influences is not the most important condition in fixing the annually recurrent pattern of change. Rather, they serve to strengthen the idea that annual and seasonal patterns of change are determined by influences of so great magnitude that they operate demonstrably in localities differing not only in geographic position, but also in numerous conditions affecting production. Local conditions in La Jolla Bay may cause modifications of details of the general annual pattern, but they do not obliterate it. The slightly more erratic occurrences of individual periods of abundance ("pulses") in La Jolla Bay also support this view because of their evidence of temporary responses to localized intensity of more or less closely restricted influences, or particular combinations of influences.

Although the patterns of annual change at the two stations show a discernible likeness in producing dinoflagellates most heavily from April to August, inclusive, there is a fairly regular discernible difference which is almost as interesting, i.e. the earlier exhibitions of annual increase of abundance in La Jolla Bay (cf. Fig. 4). This tendency to earlier increases in abundance of phytoplankton at La Jolla has been mentioned previously in a partial report on plankton diatoms for the first ten years (Allen 1936). The differences between the two stations in respect to dinoflagellates were not so distinct as in respect to diatoms, but they were observable.

Stated in general terms, the foregoing evidence appears to warrant the conclusion that the annual pattern of change is determined by influences primarily solar in origin while the outstanding departures from this pattern are determined by influences ordinarily (or at least immediately) terrestrial in origin. Even the hypothesis of biological cycles characterized by vernal increases and autumnal declines in populations is consonant with this conclusion because of the fact that cycles of this type must have been established originally under solar influences and afterwards maintained by them. Among the terrestrial influences responsible for departures from the annual pattern, and for differences between the two stations such as those noted, topography of sea bottoms and forms of shore lines must be rated highly, especially when considered as influencing characters of currents and turbulences in connection with the fundamental feature of rotation of the earth. Climatic changes and weather conditions, especially precipitation and run off, should not be neglected when considering erratic occurrences of numbers in populations as related to either time or space. And, of course, biological conditions are always basically important in some way. So far as the organisms under special observation are concerned, the season may be favorable, the delivery of solar energy may be just right, the movements of the water masses correct, the food content of the water appropriate and high, and every other observed condition encouraging, and yet there may be failure to produce abundance for the simple reason that propagative ("seed") organisms are absent. Even if they be present, they may be too few, or too feeble, or too sluggish to produce abundantly at the favorable period. Contrariwise, abundance may be missed in the presence of a viable population because some one or more of the solar, or of the physical terrestrial conditions are deficient or unfavorable. Also

predatory organisms may decimate a good seeding population before it can develop notable abundance. That is to say, there are plenty of reasons why departures from the annual pattern of abundance at any station may occur, and it is probable that in no two instances are the reasons for the departures precisely the same in all details. However, the fact that certain departures (e.g. the totally low productive years 1926 and 1931) occur similarly at two stations over one hundred miles apart indicates that certain combinations of terrestrial influences may be identified eventually if not immediately.

In addition to likenesses and differences of single years at one station, or at the two stations, there was an interesting grouping of years in the twenty year period. For the first ten years, La Jolla appears to have (Fig. 6) a slightly

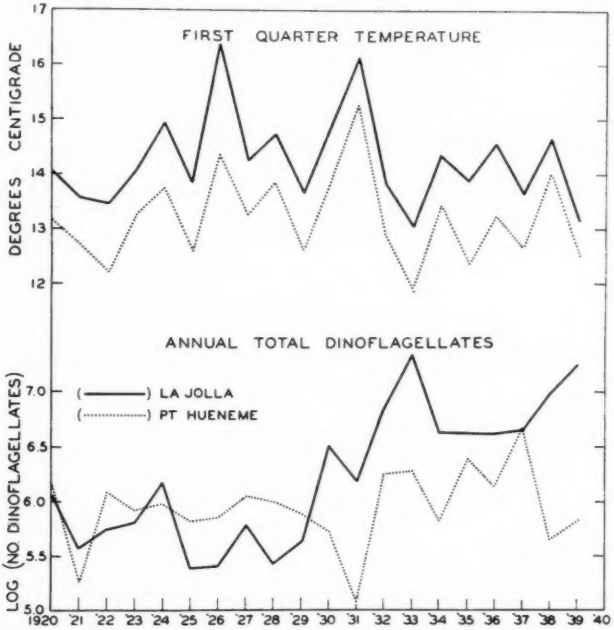

Fig. 6. Graphic representation of possible five and ten year periodicities in production of total armored dinoflagellates, including possible temperature correlations.

greater productiveness in the first five than in the second five, the first five also showing greater differences between successive years. The third five shows a return to higher productiveness (although including the very low year of 1931) and there is a strong rise to high productiveness at the end of the last five after a moderate drop. If this showing of alternating five-year periods of

greater and lesser abundances indicates genuine cycles, their existence is likely to be related to five-year weather cycles of some kind. As a matter of fact, the change in method of collecting at La Jolla at the end of the first ten years suggests a reason for questioning the genuineness of the appearance of five-year cycles, the smaller organisms having so much more prominence after 1929. However, the subtraction of the records (for the Scripps Institution) of the small forms included under the catchall designation "*Gymnodinium* spp. (nannoplankton) does not entirely obliterate the indication of the five-year cycles and it may be that a trend to such periodicity actually existed. But, perhaps the evidence for a ten-year (or longer) period is a little stronger, especially if we consider the two stations together. To offset any suspicion that larger numbers in the records of the second ten years at La Jolla were due to change of collecting method, we find the showing of Pt. Hueneme distinctly greater for the second decade although no change had been made from the original "filtration" method of collecting. As was true of the five-year periods, subtraction of the "*Gymnodinium*" catchall numbers (nannoplankton) still leaves a distinct showing of higher abundance at La Jolla for the second ten, except for 1931 and 1935. Therefore it seems reasonable to conclude that there are tendencies to cycles of productivity of dinoflagellates in periods of five or ten years, or more (the ten years from 1920 to 1929, inclusive, possibly closing a twenty or fifty-year cycle and the following ten years marking the beginning of another). The full significance of these tendencies is not clear at present, although some relationship to climatic cycles seems highly probable.

In this connection it should be noted that a number of modifications of the annual pattern of distribution of ocean temperatures together with shifts in its sequences discernible in one year as compared with another seem to have recognizable relationships to occurrences of annual differences in the pattern of dinoflagellate production. These relationships are more easily distinguishable in the records for La Jolla pier but most, if not all, are traceable at Pt. Hueneme.

At La Jolla the fundamental year pattern for temperatures appears very simple upon first glance at a graph showing weekly averages for the twenty years, i.e. there is a gradual rise to a peak a few weeks after midyear (Fig. 2) followed by a sharper decline to the end of the year. Closer inspction shows that the condition is not quite so simple as that. In no year of the twenty was the average pattern followed exactly. For example, in 1920 there were two peaks separated by a distinct depression, the maximum finally appearing a little later than might be expected from the idea of the pattern. It is evident also that different years showed marked differences in the ascending and descending slopes. But, regardless of such differences in temperatures between years the pattern of aggregate production of dinoflagellates (Figs. 4 and 5) shows a distinct rise to a peak ahead of the week of highest temperatures. In only a few years do the modifications of this pattern involve notable abundances after peak temperatures have been reached.

It is generally understood that in the temperate zones most of the phytosynthetic activity of most land plants occurs after February and before August,

a period corresponding closely with that in which dinoflagellates show greatest constructive activity. For that reason, temperatures and accompanying conditions of the first three months of a year are likely to exert influences upon the growth of vegetation which might be traceable, even in Nature. At any rate, it seemed possible that a correlation might be found between average temperatures for the first quarter of a year and the total dinoflagellate production for that year. Herewith (Fig. 6) a graphical presentation is made to show that such a correlation is observable in respect to more than one feature, not only at La Jolla but at both stations.

First, concerning low production in individual years. High temperatures early in 1926 and in 1931 preceded a season of poor production. 1925 seems to present an anomaly, its year aggregate being similar to that of 1926 although the average temperatures for the first three months were relatively low. Possibly unusually low temperatures in December of 1924 give a clue to this problem if we knew how to follow it. In a correlation of this kind, it is not to be expected that temperature alone is operative. Rather, it is the physical and chemical complex represented by temperature which is decisive, too intricate for us to follow. In many instances where temperature is credited with the deciding influence it is little more than an indicator of a deciding influence which is confusingly indirect or complex or both.

Second, concerning high production in individual years. The correlation seems to be fairly good at La Jolla, not so good at Pt. Hueneme, although not contradicted by records for the latter. At La Jolla production was excessive in 1932 and 1933 after low temperatures. In 1938 it was excessive after a temperature average approaching the median for twenty years. In 1939 it was excessive after an average markedly lower. However, in spite of the discrepancies the evidence for a correlation is at least good enough to demand attention.

Taken by decades, the evidence for correlation appears to a little better advantage, temperatures at both stations running somewhat warmer over the relatively unproductive first ten years than over the highly productive second ten.

Supplementary Inshore Stations

At this point it seems appropriate to remark that inshore observations were not confined to the two stations (La Jolla and Pt. Hueneme). As a matter of fact, supplementary series of daily catches were run for five years or more at four other stations, i.e. Oceanside (Fig. 1, twenty miles north of La Jolla), Balboa (Newport Bay Fig. 1, seventy miles north of La Jolla), Farallone Islands Light House (off San Francisco Bay), and Scotch Cap Light House (Aleutian Islands). The Oceanside series was terminated in five years because the annual pattern of production resembled that of La Jolla so closely that the extra effort seemed unnecessary pending the development of better general understanding of phytoplankton distribution. The Balboa series was never dependable because of local difficulties of operation which led to abandonment after five years. At Farallone Light no large catch

was ever obtained and most catches were too small to be significant, a condition which led to discontinuance after five years. Difficulties of communication caused some breaks of continuity at Scotch Cap Light but the series as a whole was good for about seven years and it was dropped partly because of increasing pressure of phytoplankton routine and partly because it was felt that other institutions should be able to handle it better because of being nearer to that region. The annual pattern of phytoplankton occurrence had a considerable resemblance to that of Southern California except that the numbers of dinoflagellates were negligible throughout the period of observation (Cupp 1937). So far as the relationships to the present discussion are concerned, the main value of information from these supplementary series lies in the showing that the two standard stations are fairly representative of general conditions, trends, and fluctuations of phytoplankton occurrence and production inshore. However, the point must not be neglected that they show also distinct differences in localities in respect to these phenomena.

Short series of collections were tried in several other localities, discontinuance being due partly to difficulty of making suitable arrangements for dependable daily catches and partly to rapid accumulation of material from preferred localities. None of these short series showed any significant tendency to departure from the general pattern of annual and seasonal distribution observed at the two standard stations.

Offshore Abundance of Dinoflagellates

In a period of more than twenty years, by cruises, expeditions, and special trips, at hundreds of stations, more than five thousand catches of phytoplankton have been taken off shore at distances ranging from a mile or two to mid-ocean. Up to 1938 most of these catches were obtained from surface levels by Scripps Institution boats, ships of the U.S. Navy, ships of the U.S. Coast and Geodetic Survey, patrol boats of the Mexican Government, boats of the International Fisheries Commission and of the California Fish and Game Commission, coastwise passenger steamers, private yachts, and commercial fishing boats. Although most of the collecting was done in California waters, some hundreds of catches were made in localities ranging from Peru to Alaska, Alaska to Hawaii, and San Francisco to Australia. In and after 1938 most catches were made below the surface, six in addition to the surface at levels successively ten meters deeper. All were obtained by the Scripps Institution research ship "E. W. Scripps," using the Allen closing bottle of five liters capacity at all levels.

Dinoflagellates were obtained at nearly all offshore stations but the numbers were usually small, or even negligible. Out of the thousands of catches only about five hundred showed numbers as large as one thousand cells per liter. Many of these were at distances of five or ten miles from shore but less than fifty were more than thirty miles from shore. None were as much as one hundred miles from shore. Apparently, dinoflagellates thrive best in localities fairly near shore, at least so far as waters of the eastern North Pacific Ocean

are concerned. This tendency to lower abundance far offshore in Pacific waters is shown also by the fact that no catch as large as 25,000 cells per liter was taken as far as twenty miles from shore. Even in the Gulf of California only one station showed as many as 100,000 cells per liter as far as thirty miles from shore. Apparently, the "red water" abundance of more than a million cells per liter, sometimes observed at piers or near shore, occurs only rarely, or never, at distances more than twenty miles to seaward.

Depth Distribution

Because less than one thousand catches were taken at any particular level below the surface in the boat collections of the twenty year period, and because the time and locality relationships of these catches at any particular level were not demonstrably identical, or even completely comparable, no conclusive generalizations are warranted by the evidence. On the other hand, this evidence seems to present reasonably dependable support for some provisional suggestions.

Although not entirely convincing, available evidence suggests rather strongly that the surface level (above five meters) is usually representative of conditions at boat stations even when the greatest single catch is made at some other level. Aside from the possibility that the ten meter level tends to show *extreme* abundance a little more often it appears probable that the surface level leads in *significant* numbers of armored dinoflagellates more often than any number. However that may be, it is clear from the data that large abundance, or locally superior abundance, is rarely found at or below thirty meters. Even in the Gulf of California, highest abundance at a strongly productive station (1939, Sta. 48, 168,000 cells per liter) has been found as low as thirty meters in only one instance and the next to highest abundance (Sta. 51, 209,000) at that level in one other instance.

No such relationships have been observed in the open sea off the California coast where most of the collecting beneath the surface has been done. That is to say, really significant numbers of armored dinoflagellates have not been observed below thirty meters and very few locally superior numbers at or below that level. Tendency to decline of production below thirty meters is shown also by the occurrence of catches equalling or exceeding 1,000 cells per liter. Of such, eighteen were found at thirty meters, twelve at forty, nine at fifty meters and three at sixty meters.

Locality Distribution

Although differences between certain inshore stations and between inshore and offshore stations in respect to productivity have been mentioned in preceding pages it seems desirable to emphasize the irregularities of distribution as revealed by use of sea going vessels Even the crude collecting by tow nets used for phytoplankton in 1917 and 1918 showed clearly that catches from different stations off shore were not alike in the numbers of organisms

obtained. For example, no two of the eighteen stations sampled in the Institution cruise in the Gulf of Santa Catalina in 1917 were alike in the numbers of dinoflagellates caught. Indeed the numbers of species represented were different at most of them (Allen 1921a, Table I). The hundreds of stations sampled since that time by the more accurate methods of the Allen Filtration Net and the Allen Closing Bottle have yielded evidence substantially similar to this. Therefore, it seems to be reasonable to conclude that localities offshore tend to differ among themselves in the numbers present at any particular time and that those showing significant numbers differ in total numbers produced in a particular season or year. The evidence is not so strong for dinoflagellates as it is for diatoms (on account of smaller numbers) but it points to the same conclusion.

Especially interesting items concerning differences between offshore stations were obtained from stations 1 and 2 (respectively ten and five miles offshore from the Scripps Institution) which were sampled frequently in the years 1921, 1922, 1923, 1924, 1926, and 1927. Series of catches at a number of depths were taken at these two stations on the same days, usually within a very few hours of each other, thus making the catches as nearly comparable as is possible by use of only one boat. Except in the series when catches at both stations were too small to have numerical significance the numbers found at one were never the same as those found at the other. On thirty-two days of collecting in 1921, Station 2 gave some evidence of more production of dinoflagellates, numbers above 300 cells per liter being found on ten days as compared with four days at Station 1. However, Station 1 yielded over 2,000 cells per liter on June 22 when less than 300 were taken at Station 2, thus indicating that while a few samples may show differences between stations they do not necessarily reveal the extent or the characteristics of the differences. In 1922, Station 1 was more nearly like Station 2 in the number of significant catches (19 to 23) but it was far inferior in the size of catches. Through the shorter period of sampling in 1923 the two stations were not strikingly different, although there appeared to be a slight reversal in favor of Station 1. Through the longer period from mid-May to late August in 1924 there was a definite showing of better production at Station 2 (Sleggs 1927). After the Kofoid Closing Bottle was displaced by the lighter Allen Closing Bottle in 1926 collecting was done much more quickly and effectively and comparisons of abundance at the two stations became even more dependable than they had been formerly. Again production of dinoflagellates appeared definitely superior at Station 2 although the numbers of diatoms were smaller there throughout the series. An offshore cruise in August showed the numbers of dinoflagellates to be practically negligible from one end of the Gulf of Santa Catalina to the other in all stations to seaward, much too small for trustworthy comparison of production at different stations. Results of collections in 1927 emphasized those for 1926, Station 2 (five miles) showing larger abundances than Station 1, (ten miles) regularly throughout the summer series. Thus the evidence from off shore appears to be equally convincing with that from inshore in support of the idea that abundances of dinoflagellates are generally unlike at different stations.

Indeed, there is strong indication that stations differ in annual totals of production. While for the dinoflagellates there is a suggestion that the more prominent differences in annual production may be related to distances from shore of the stations sampled, it remains reasonably certain that locality differences are observable between stations far off shore and that those differences have little, if any relation to linear distances from shore.

Taxonomic Limitations

At first thought, it might be supposed that twenty years of acquaintance with dinoflagellate populations represented in series of collections widely ranging in the Pacific Ocean would result in the accumulation of a long list of names of component species. On the other hand, it does not require much experience to show that accurate naming of new species or invariably accurate determination of most species is impossible if progress is to be made in quantitative studies of general populations in Nature. Consequently, with few exceptions, the names appearing in the phytoplankton records of the Scripps Institutions are tentative approximations intended to suggest the ranges of variety in the populations or to facilitate the tracing of distinguishable forms through times and spaces. Sometimes, also, names of doubtful appropriateness were recorded in order to have a guide to particular material in case opportunity appeared or necessity arose for critical treatment. Under such limitations the following incomplete and largely suggestive list of eleven genera and forty-one species has been assembled. It is quite reasonable to suppose that many other genera and at least three times as many species were actually represented in the more than twenty thousand samples of phytoplankton examined microscopically.

Dinoflagellates Listed at Scripps Institution

(Naming according to Schiller 1933)

Ceratium
- *arietinum* Cl.
- *azoricum* Cl.
- *candelabrum* (Ehr.) Stein
- *contortum* (Gour.) Cl.
- *extensum* (Gour.) Cl.
- *furca* (Ehr.) Clap. et Lach.
- *fusus* (Ehr.) Duj.
- *Kofoidii* Jörg.
- *lineatum* (Ehr.) Cl.
- *longipes* (Bail.) Gran
- *longirostrum* Gour.
- *macroceros* (Ehr.) Cl.
- *pentagonum* Gour.
- *pulchellum* B. Schr.
- spp.
- *trichoceros* (Ehr.) Kof.
- *tripos* (O. F. Müller) Nitzsch.

Dinophysis
- *acuminata* Clap. et Lach.
- *acuta* Ehr.
- *arctica* Meresch.
- *caudata* Sav-Kent.
- *ellipsoides* Kof.
- *hastata* Stein
- spp.

Goniaulax
- *catenalla* Wh. and Kof.
- *polyedra* Stein
- spp.

Gymnodinium
- spp.

Noctiluca
- *miliaris* Sur.

Oxytoxum
- spp.

Peridinium
- *crassipes* Kof.
- *depressum* Bail.
- *divergens* Ehr.
- *globulus* Stein

granii Ostf.
minutum Kof.
oceanicum Vanhöffen
pentagonum Gran
pyriforme Pauls.
spp.
steinii Jörg.

Phalacroma
rudgei Mur. and Wiht.

Podolcmpas
bipes Stein

Prorocentrum
dentatum Stein
micans Ehr.

Pyrocystis
lunula Schütt

So far as the records for twenty years are concerned only seven species representing four genera ever reached large abundance or a commanding lead in production. These include one species of *Goniaulax* (*G. catenella* Whedon and Kofoid) and the only recorded species of *Noctiluca* (*N. miliaris* Suriray), which were prominent only in the Gulf of California. *Ceratium fusus* (Ehr) Duj. was never dominant in leadership even at greatest abundance and *Goniaulax polyedra* Stein was excessively abundant only in 1939, one year in twenty. For most of the twenty years the totals of dinoflagellate production were mainly dependent upon three species i.e. *Ceratium furca* (Ehr) Clap et Lach, *Ceratium tripos* (O. F. Müller) Nitzsch, and *Prorocentrum micans* Ehr. Of the three the latter was much the most prominent in spite of its great inferiority in size. Other species encountered with frequencies sufficient to keep them well in mind as components of the dinoflagellate populations were: *Ceratium azoricum* Cleve, *C. candelabrum* (Ehr) Stein, *C. Kofoidii* Jörg., *C. macroceros* (Ehr) Cleve, *C. pentagonum* Gour., *C. tripos* (O. F. Müller) Nitzsch, *Dinophysis acuminata* Clap. et Lach., *D. caudata* Sav.-Kent, *D. ellipsoides* Kof., *Gymnodinium* spp., *Noctiluca miliaris* Sur., *Oxytoxum* spp., *Peridinium crassipes* Kof., *P. depressum* Bail., *P. divergens* Ehr, *P. Granii* Ostf., *P. oceanicum Vanhöffen*, and *P. Steinii* Jörg.

Outstanding Species

One unexpected result of the twenty years of daily observations at La Jolla and Pt. Hueneme piers was the finding that only four species of dinoflagellates could be rated as outstanding for the period as a whole. In order of perennial prominence these were *Prorocentrum micans* Ehr., *Ceratium furca* (Ehr.) Clap. et Lach., *C. tripos* (O. F. Müller) Nitzsch, and *Goniulax polyedra* Stein, but only the first and last named ever became so excessively abundant as to be primarily responsible for extensively conspicuous occurrences of "red water." Under the obligatory conditions of enumeration the identity of all of these species was often uncertain, especially when the numbers were small or the characteristics highly variable.

PROROCENTRUM MICANS Ehr. Although it was the smallest of the four conspicuous species, *Prorocentrum micans* Ehr. (Fig. 3) rarely caused definite uncertainty as to identification except for the occasional presence of a still smaller form about half as large as the one most common. The smaller specimens were never very numerous and they were included in the records with the others.

P. micans Ehr. was represented in La Jolla Bay in every year of the twenty

but not at Pt. Hueneme in 1935, and the total numbers for the year were extremely low in 1925, 1926, 1928 and 1931. The extreme height of total annual production was reached in La Jolla Bay in 1939 (Fig. 7) with other notably

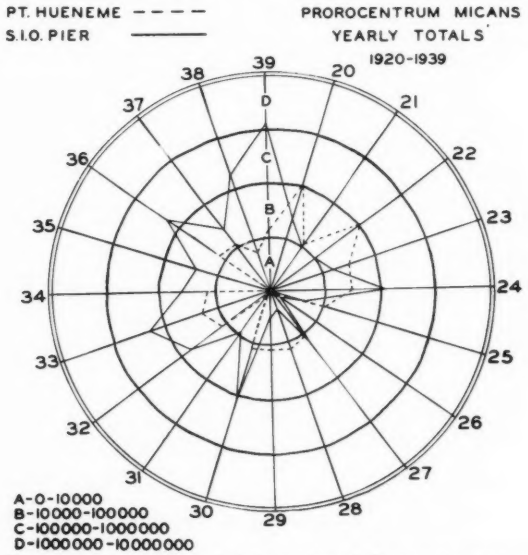

Fig. 7. Total numbers per liter of daily catches of *Prorocentrum micans* for each of twenty years; to show fluctuations of abundance by year periods, also larger numbers at La Jolla after changing methods.

productive years in 1924, 1930, 1933, 1936, 1938, 1939, (Fig. 7) in three of which (1924, 1933, and 1939) the showing of high production was due largely to single cases of "red water." At Pt. Hueneme only the years 1920 and 1922 produced totals large enough to attract particular attention and at no time in the twenty years was "red water" recorded there. The annual pattern of production, as determined by adding numbers for all of the twenty years for successive periods of four weeks (Fig. 8), was very much like that for total dinoflagellates, as might be expected because of the high prominence of this species in dinoflagellate populations. According to this pattern the summer season is most favorable in most years.

The relationship of *P. micans* Ehr. to evidence of ten year periodicity for dinoflagellate annual totals requires attention. Even more striking than for all dinoflagellates combined is the preponderance of this species at La Jolla in the second ten years, as compared with the first ten. But, this showing corresponds exactly with the change to the settling method of collecting at La Jolla. A suspicion that this condition invalidates the evidence offered in preceding pages as indicating five, ten, or twenty year periodicities arises necessarily. How-

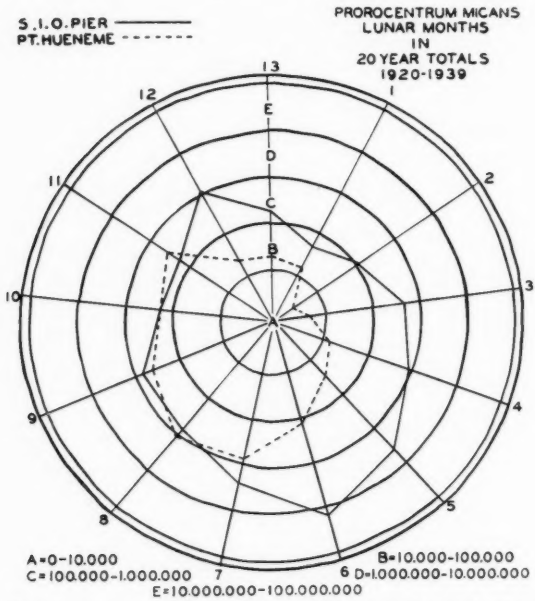

Fig. 8. Twenty years totals of numbers for each four week period ("lunar month") of annual thirteen; to show higher abundance in summer in year pattern of *Prorocentrum.*

ever, it should be remembered that *P. micans* Ehr. is strongly adhesive and cohesive and that the loss through a filtration net is much less when numbers are very large. Therefore, the representation in catches of more productive years might have been expected to be more nearly complete than in less productive years even if filtration collecting had been continued. That is to say, it still remains probable that the difference between the two ten year periods was real although less extreme than indicated by the records. Also the decline in the second five years occurred before methods of collecting were changed, thus indicating some tendency to periodic fluctuation. In addition, catches of larger forms of dinoflagellates showed increase in the second ten years and it is not certain that *P. micans* Ehr. carried enough influence to invalidate the evidence for greater production in the second ten years. Furthermore, it should be remembered that temperatures (p. 25) appeared to be more favorable for total dinoflagellates for the second ten years. Still, there is room for reasonable doubt for total dinoflagellates as well as for this particular species, if one prefers to entertain it. Exhaustive analyses of existing data might solve the problem but that is impossible at present.

Aside from problems of its periodicity and relative abundances, *P. micans* is interesting because it is the only armored dinoflagellate which has been

shown to be extensively used as food by California sea mussels (Fox 1936). It is mentioned by Lebour (1925) and by Schiller (1933) as a source of food for mussels, oysters, and other shell fish. Lebour also says that pilchards and other fishes feed upon it extenisvely. If it has recognizable value as food for these groups of sedentary and natant animals it may be supposed to have similar value as food for other groups, perhaps many of them. Especially is it natural to suspect that numerous kinds of plankton animals feed upon it.

CERATIUM FURCA (Ehr.) Clap. et Lach. *Ceratium furca* ranked second in constancy of representation along shore, especially at the Scripps Institution pier. Not only was it found in many single catches in every year of the twenty but it was recorded in at least eleven out of thirteen four week periods in nineteen out of twenty years at La Jolla Bay. Only in 1931 did the representation occur in as few as six months (four early and two late in the year). Although the largest catches were obtained usually in late Spring (Fig. 9)

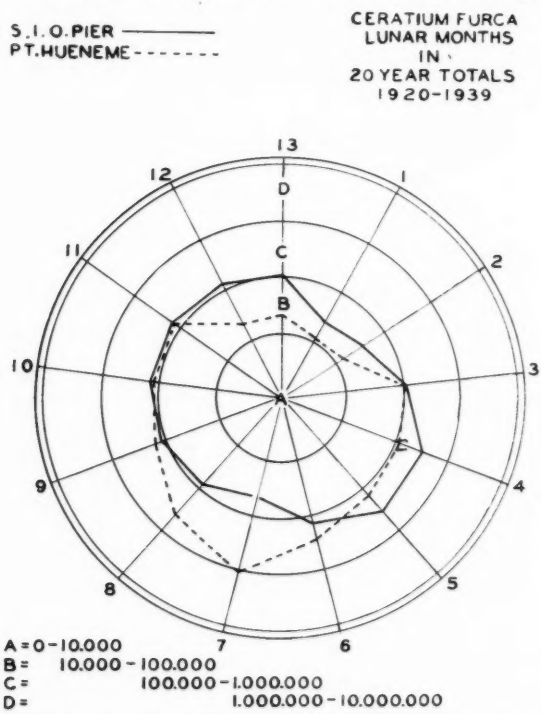

Fig. 9. Twenty years totals of numbers of *Ceratium furca* for each four week period of annual thirteen; to show higher abundance in Spring at La Jolla and Summer at Pt. Hueneme in year pattern.

abundances almost as large were found in other seasons in certain years. At Pt. Hueneme few catches (none large) were made in either of the first two months or the last two months in most years. On the other hand, there were only ten four-week periods (scattered through the aggregate two hundred and sixty) in which none were recorded, no single year in which representation so nearly failed as at La Jolla in 1931. The annual pattern of occurrence showed largest abundance a little later than at La Jolla (Fig. 9). Total numbers for twenty years were nearly fifty percent larger at Pt. Hueneme than at La Jolla.

In the thousands of catches from widely different localities, it is probable that ninety-five percent of the specimens conformed fairly closely to the diagrammatic sketch shown in Fig. 3. There could be no doubt of their close relationship to the species even if some may have been separable from it by more or less nearly exhaustive study.

CERATIUM TRIPOS (O. F. Müller) Nitzsch. *Ceratium tripos* (Fig. 3) ranked third in constancy of representation at both stations. Only in 1931 was it absent from the records in more four-week periods than it was present. Numbers were small (most often, none) in January and December of most years. Indeed, there were few years in which the abundances were more than negligible in the first and last weeks at La Jolla and the first and last twelve weeks at Pt. Hueneme. Stated in another way, there was a distinct tendency toward better production in the period from mid-April to mid-October at La Jolla and from mid-May to mid-October at Pt. Hueneme. Strangely enough, in view of the shorter period, the latter station showed a total production for the twenty years which was more than twice as large as that for the other. The annual pattern (Fig. 10) shows definitely not only the winter thinness of populations and the summer high productiveness but it shows the later period of production at Pt. Hueneme. Apparently, this species, more than any other of the four, tends to conform to seasonal periodicities and to their modification by latitudinal influences.

Identification of *C. tripos* was often highly unsatisfactory. Not only is this species extremely variable but so are a number of close allies. Nevertheless, it seems reasonable to assume that more than half of the identifications were correct and that the others were close enough for general purposes. Certainly most of the specimens observed conformed fairly well to the diagrammatic outline in Fig. 3. This is the largest species of the leading four (Fig. 3) and it might be expected to contribute notably to the food supply of small animals, but the Scripps Institution has not obtained any evidence to support that expectation and the literature contributes none.

GONIAULAX POLYEDRA Stein. *Goniaulax polyedra* (Fig. 3) is only a little larger than *Prorocentrum micans* Ehr., with which it shares the primary responsibility for occurrences of "red water" along the California coasts. Unlike the latter, or either of the two *Ceratiums*, *G. polyedra* is decidedly erratic in occurrences, missing any recording throughout whole years at both stations, notably 1923, 1927, 1931, 1936, and 1939. In several other years the occurrences were very few or the numbers very low. The showing for high

abundances was still worse. Only at La Jolla was conspicuous abundance reached and there only in 1932 and 1938. At Pt. Hueneme, 1926 and 1937 were the only years in which total numbers for a four-week period exceeded 100,000 cells per liter. Indeed, the rank among the leaders depends mainly on the prominent "red water" at La Jolla Bay and off San Diego in June 1939, although production was very high in the La Jolla locality in October and November 1932. Because of the erratic occurrence and rarity of excessive production it is necessary to view the graphic representation of the year pattern (Fig. 11) with considerable caution. The indication of summer increase at La Jolla (even the late summer increase at Pt. Hueneme) corresponds moderately well with tendencies shown by the other leading species but the high productivity indicated for three four-week periods late in the year at La Jolla is surprising. However, reference to manuscript tabulations proves this to be mainly dependent on 1932, with recognizable trends in that direction in five other years, trends somewhat more definite at Pt. Hueneme. Evidently, the twenty-year period is too short to establish conclusively a year

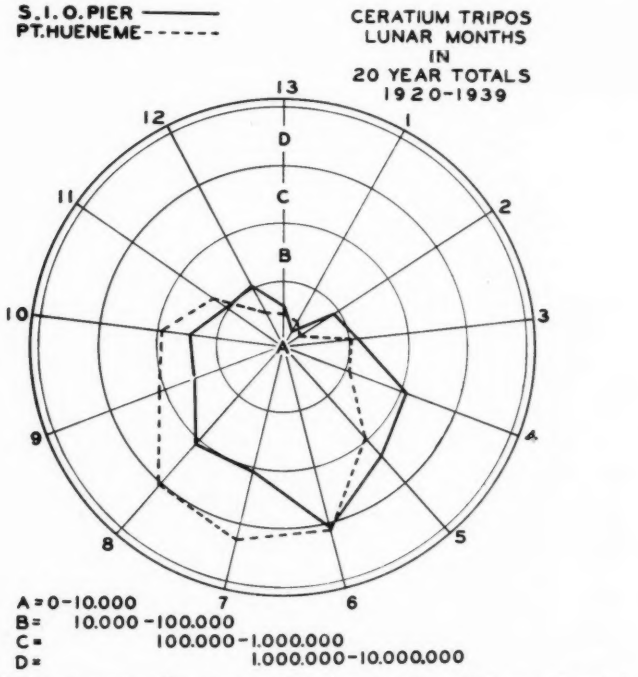

Fig. 10. *Ceratium tripos*. Twenty year totals of numbers for each four week period of annual thirteen; to show strong preference for warmer seasons in year pattern.

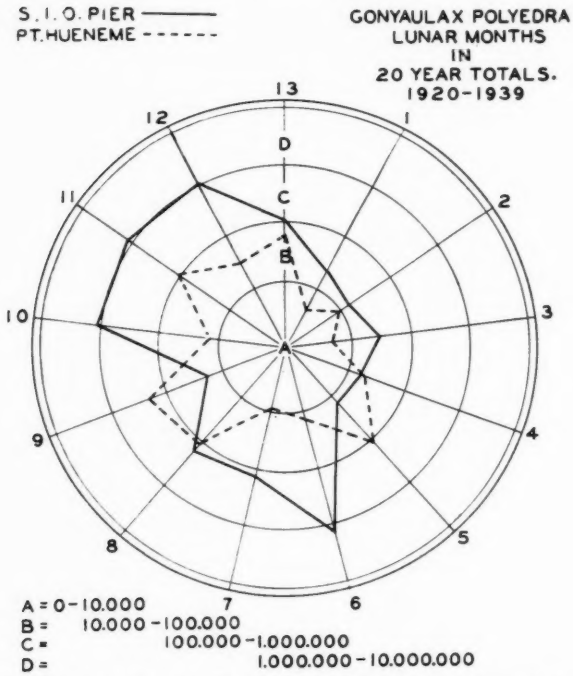

Fig. 11. *Goniaulax polyedra.* Twenty year totals of numbers for each four week period of annual thirteen; to show peculiar year pattern of a species occurring erratically.

pattern for a species so erratic in occurrence as *G. polyedra.* On the other hand, the tendencies seem definite enough to warrant expectation that this pattern will be approached more often than any other in future years.

Like the two *Ceratiums, G. polyedra* has not yielded evidence of importance as a contributor to the fundamental food supply of the sea. Nevertheless, a number of records indicate an important relationship to animals at certain times and under particular conditions. Because of the reports by Torrey (1902) and others, this species has acquired a bad reputation for injury to marine animals, including fishes, when it appears in such abundance as to cause "red water." The absence of recognizable lethal effects on animal populations in and near La Jolla Bay in "red water" of 1939 suggests that mere occurrence of that phenomenon is not sufficient to cause widespread destruction of marine animals. Apparently, there must be contributing causes to accompany it in producing lethal effects. However, it should be remembered that Sommer, Whedon, Kofoid, and Stohler (1937) have identified

a closely allied species of *Goniaulax* (i.e. *G. catennella* Whedon and Kofoid) as a cause of "mussel poisoning." Perhaps no *Goniaulax* is harmful to man or to marine animals ordinarily, but only under specific conditions. Still, possibilities of injury are little less interesting than probabilities. Therefore, *Goniaulax* is likely to hold a prominent place because of its evil reputation.

Identification of *G. polyedra* was rarely positive although usually probable. The small size impaired observation of essential details and the rounded form was responsible for confusing differences of positions of specimens on the slide. In addition, there was enough of resemblance to allied species and to *Goniodoma polyedricum* (Pouchet) Jörgensen to cause more or less confusion in certain cases. On the other hand, so many specimens appeared to be recognizable that the percentage of error must have been small. The diagrammatic sketch in Fig. 3 indicates the general appearance of Scripps Institution specimens.

Summary

1. Hundreds of catches from widely different localities and regions in the Pacific Ocean show definitely that dinoflagellates may be found almost anywhere, and thousands of catches taken daily at limited numbers of stations over periods of five to twenty years show just as definitely that the numbers are rarely very large, mostly below thousands per liter in most localities.

2. At the two standard stations, La Jolla and Pt. Hueneme, only four species of armored dinoflagellates attained outstanding prominence. Of these, only *Prorocentrum micans* Ehr. and *Goniaulax polyedra* Stein ever became so excessively abundant as to cause "red water": *Ceratium furca* (Ehr.) Clap. et Lach. and *C. tripos* (O. F. Müller) Nitzsch were prominent because of constancy of representation in at least moderate numbers.

3. Daily observations in La Jolla Bay over a period of twenty years gave ample opportunity to note the streakiness and patchiness of surface distribution of dinoflagellates, *Prorocentrum* in particular, its streakiness often showing on the surface where it was easily visible.

4. Some thousands of catches obtained by systematic cruising at sea by the Scripps Institution have shown that large production of armored dinoflagellates is confined almost entirely to levels above thirty meters depth and to a zone within twenty-five miles of shore. So far, no "red water" has been observed as far off shore as thirty miles in Southern California waters.

5. The daily catches at the two standard stations have yielded evidence suggesting five or ten year periodicities in productivity. They show also fairly good conformity to a year pattern of summer increase and winter decrease in production.

6. The Scripps Institution's adaptation of the measured water method has proven to be highly satisfactory in collecting armored dinoflagellates, *a closing bottle being used for sampling when working from a boat offshore.*

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Seasonal Food-Cycle Dynamics in a Senescent Lake*

Raymond L. Lindeman

"Large fish eats small fish;
Small fish eats water insects;
Water insects eat plants and mud."
—Chinese proverb.

Introduction

The problem of trophic relationships has long been recognized as a central influence in the field of limnology; few attempts have been made, however, to analyse the quantitative seasonal dynamics of these relationships. The existence of food-chains has been known since the earliest civilizations; the cyclic nature of food-relations, recognized with the earliest development of exact chemistry, was originally clearly stated by Lavoisier (Henderson, 1913). The detailed analysis of trophic relationships has been initiated much more recently, accompanying the development of limnology as a science. A piscian food-chain similar to that of the above apothegm was described in detail by Forbes (1887) in his classical essay, "The Lake as a Microcosm." The brilliant exposition by Forel (1904) of the general nature of food cycles (dissolved mineral nutrients, autotrophic plants, herbivores, carnivores, bacteria and back to dissolved nutrients) will serve even today as an introductory account of trophic relationships. Subsequent research, until very recently, has been concerned largely with qualitative rather than quantitative aspects of these fundamental community phenomena.

The careful study of food cycles reveals an intricate pattern of trophic predilections and substitutions underlain by certain basic dependencies; food-cycle diagrams attempt to portray these underlying relationships. Insofar as certain members of the food-group units may occasionally vary their diet, particularly toward the predatory ends of the food-chains, all trophic diagrams are somewhat Procrustean.

Various attempts have been made to diagram the general trophic relations in aquatic habitats. The first of these, by Shelford (1913), graphically portrayed the food-chains described by Forbes in 1887. Alsterberg (1924) diagrammed a cycle including nutritive regeneration from benthic ooze by action of the tubificid "sediment-transporters." The first really comprehensive

* This is the third in a series of papers, "Ecological Studies of a Senescent Lake," describing various ecological aspects of Cedar Creek Bog, Minnesota. This paper represents a portion of a thesis submitted to the Graduate Faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

diagram of aquatic food cycles was given by Thienemann (1926) in his essay, "Der Nahrungskreislauf im Wasser"; his figure has been modified slightly in the publications of Perfiliev (1929) and Welch (1935). Strøm (1928) published a food-cycle diagram emphasizing the central position of ooze in trophic cycles, as well as the relation of autochthonous to allochthonous nutritives. Rawson (1930) developed a diagram of similar nature, with primary emphasis on the trophic relations of fishes. Wasmund (1930) presented a complex diagram of lake metabolism which emphasizes the relation of allochthonous detritus and dissolved nutrients to stratigraphy and to human influences.

The food-cycle relationships in small senescent lakes, because of such features as relatively uniform depth, general homogeneity of bottom type and absence of violent wave action, tend to be less complicated and more easily studied than those of large lakes. Yet nearly all features of the food-cycle diagram (Fig. 1) resulting from the study of such a lake (Fig. 2) can be applied directly to the earlier eutropic stage of aquatic succession.

Dissolved nutrients, autochthonous and allochthonous, are incorporated into organic substances by producers, of which three types are common in

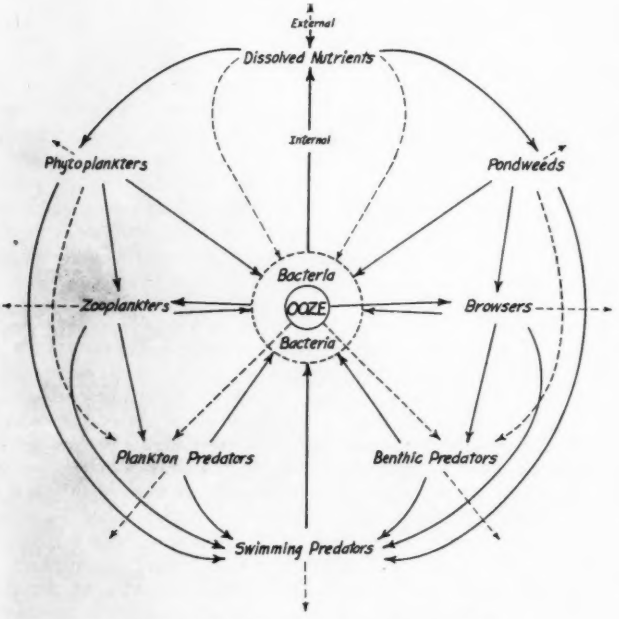

Fig. 1. Food-Cycle Relationships in a Senescent Lake.

lakes: *autotrophic bacteria, algae* and *pondweeds*. Each of these may die and decompose by bacterial action into ooze, or may be eaten by some consumer. *Zooplankters* feed as primary consumers upon phytoplankton algae, bacteria and particulate organic matter; they in turn may be eaten by secondary consumers, such as *plankton predators* and small *swimming predators*, or they may die and contribute to the benthic ooze. Plankton predators, as the name implies, feed mostly on zooplankters, although some phytoplankters and some ooze particles also may be consumed. As secondary consumers, they may be eaten in turn by such tertiary consumers as larger swimming predators, they may pupate and leave the aquatic community as adult insects, or they may die and contribute their substance to the ooze by bacterial action.

Pondweeds, synthesizing organic substance from dissolved nutrients, may act as food for many kinds of consumers, or may decompose by bacterial action into ooze. Jacot (1940), to whom the author is indebted for the concept of successively remote consumer groups, considers saprophages as "low primary" consumers. Certain animals feed directly on pondweeds as herbivores (primary consumers); others feed upon the decomposing plant tissue, or nascent ooze. These two groups have overlapping food habits and are most conveniently grouped together in the food cycle diagram. These primary *browsers* are in turn fed upon by secondary consumers, *benthic predators*, and tertiary consumers, *swimming predators*. Secondary consumers may also feed to a certain extent as primary consumers, eating small quantities of green plant tissue and even benthic ooze. Tertiary and quaternary consumers, such as swimming predators, may obtain nutriment from any of the lower consumer groups of the food cycle. Small quantities of green plant materials appear to be eaten by even rather remote predators, although this usually constitutes a very small fraction of the diet. In a general way, the more remote a consumer becomes with respect to the primary sources of food (producers), the more versatile are its food habits. The substance of each group upon death of the organisms contributes to the benthic ooze, from which plant nutritives are again dissolved.

The relationships of consumer food habits to community structure were greatly clarified as a result of the concepts presented by Elton (1927), who stressed the importance of size and of numbers in the animals of a community. Beginning with primary consumers of various sizes, there are as a rule a number of food-chains radiating outwards, in which the predators become successively larger, while the parasites and hyperparasites are progressively smaller than their hosts. Since small primary consumers can increase faster than larger secondary consumers and are so able to support the latter, the animals at the base of a food-chain are relatively abundant while those toward the end are progressively fewer in number. The resulting arrangement of sizes and numbers of animals Elton termed the Pyramid of Numbers. The quantitative dimensions of this Consumer Pyramid depend upon the physiological efficiency of the groups at various levels and the extent to which the consumers at higher levels partake of the food of lower groups.

Area Studied

During the past five years the author has been engaged in an intensive study of Cedar Bog Lake, which represents a late stage of eutrophic senescence (see Fig. 2). The lake originally occupied a rather large ice-block

Fig. 2. Midsummer aspect of Cedar Bog Lake, July 16, 1937.

depression in the Anoka Sand Plain; sedimentation and marginal vegetational invasion, however, have reduced Cedar Bog Lake to less than 1/10 of its original depth and area. The lake at present has a maximum depth of about one meter, an aquatic area of 14,480 square meters, and a "shore line" of 500 meters. The developmental history of the lake is described in the first paper of this series (Lindeman, 1941).

In the following pages we shall discuss first the qualitative food-cycle relationships in the lake, and then attempt to analyse the quantitative seasonal dynamics and the productivity aspects of these relationships.

Qualitative Food-Cycle Relationships

Dissolved nutrients, consisting of those chemical elements considered essential for life (N, P, S, K, Ca, Mg, Fe, Mn, B, Zn, Cu), usually in ionic form, are supplied to the senescent lake from three main sources: (1) drainage and seepage into the lake from the surrounding drainage basin; (2) regeneration from organic ooze by action of heterotrophic bacteria; and (3) excretion of dissolved substances into the water by the aquatic organisms. That the first source may at times be considerable is attested by the fact that, following the spring thaw of 1937, sufficient water drained into

the lake from the surrounding bog to actually double the volume of water in the lake. Unfortunately no data are available as to the amounts of these allochthonous nutrients. A few data on the action of heterotrophic bacteria are discussed on page 650.

Autotrophic bacteria are probably of considerable importance as producers of organic substance in lakes (Henrici, 1939). Since these have not been studied in Cedar Bog Lake, they are mentioned here simply as hypothetical members of the food cycle. Certain colorless flagellates, which are apparently both autotrophic and anaerobic, appear in the lake during winter stagnation (Lindeman, 1942a).

Phytoplankters in the open water of the lake varied considerably, both in quality and quantity, throughout the year. The net phytoplankton consisted largely of dinoflagellates: *Ceratium hirundinella* (O. F. Müller) was present throughout the warmer months of every year, reaching in 1940 a maximum abundance of 6 gm/m^2 dry weight,* (VII-27-40), while in 1939 (VI-15-39) a tremendous "bloom" weighed more than 10 gm/m^2; species of *Peridinium* also occurred, but never reached the abundance of *Ceratium*. Blue-green phytoplankters, such as species of *Anabaena, Aphanocapsa, Aphanizomenon* and *Oscillatoria,* were common during the summer, but on only one occasion (VIII-15-38), did these forms approach "bloom" frequencies. The diatoms *Melosira* and *Synedra* were conspicuous at times, particularly during late autumn. The green flagellate *Eudorina elegans* Ehr. was common during the summer of 1940.

Nannoplankters (the micro-algae capable of passing through the meshes of a plankton net) are usually far more important to the metabolism of a lake than are the larger plankters. At nearly all seasons, but particularly during spring and late autumn, the weight value of nannoplankters in Cedar Bog Lake far outranked that of the larger phytoplankters. The chief genera involved in this tremendous production, which often exceeded 5 gm/m^2 dry weight, were *Scenedesmus, Westella, Micractinium* and *Actinastrum.*

The role of phytoplankton in lake metabolism cannot be over-emphasized. The nannoplankton, of course, is one of the chief sources of food for planktonic rotifers and entomostracans. The larger phytoplankters such as *Ceratium, Eudorina,* etc. may also serve as food for the zooplankton. It seems probable that these larger phytoplankters, in addition, serve as food for the plankton predator, *Chaoborus,* as well as for small fishes. In larger eutrophic lakes, and to a lesser extent in Cedar Bog Lake, the phytoplankton is the major source of the benthis ooze upon which the ooze browsers subsist.

The **zooplankters** of Cedar Bog Lake, except during late winter and early spring, consisted largely of rotifers. *Keratella cochlearis* (Gosse) was the most abundant species, increasing in numbers throughout the summer to an autumnal maximum of ca. 2 gm/m^2 dry weight in 1937. Other genera common during the summer months were *Brachionus havanaensis* Rousselet,

* The weight values of all organisms are expressed as gm/m^2 of surface area in order to facilitate productivity and efficiency calculations.

Polyarthra trigla Ehr. and *Synchaeta* spp. *Filinia longiseta* (Ehr.) seemed most tolerant of inimical winter conditions, surviving long periods of anaerobiosis, and appearing as the most common rotifer in winter and early spring. Many other genera inhabited the pondweed zone of the lake, but these "pseudoplankters" have not been especially studied. Species of the copepod *Diaptomus* were common only during the late autumn and winter of 1938-39 and 1939-40, reaching a maximum frequency during January of ca. 0.5 gm/m^2 dry weight.

These zooplankters are primary consumers, feeding indiscriminately upon nannoplankters and suspended organic particles less than 10μ in diameter (Naumann, 1923; Myers, 1941). The suspended excrement of zooplankters may be readily attacked by aerobic bacteria to release considerable amounts of dissolved nutrients. The bodies of dead zooplankters likewise may be attacked by aerobic bacteria as they settle toward the bottom. The substance of dead plankters furnishes nutriment for the many benthic ooze browsers; it is finally attacked by benthic bacteria, which further dissolve the softer tissues to release nutrient salts. More resistant structures such as jaws and loricae of rotifers, spines and ephippia of cladocerans, etc., may persist as semi-fossils buried deep in the ooze. The living zooplankters, particularly the copepods, fall prey to larvae of *Chaoborus* and to small fishes; rotifers, being smaller in size, are less frequently eaten by these forms.

Plankton predators in the open water of the lake consist largely of the "phantom larvae" of *Chaoborus punctipennis* (Say), which at times are tremendously abundant. These larvae are primarily predatory, feeding on zooplankters (Frankenberg, 1915; Eggleton, 1931) and small benthic organisms (Muttkowski, 1918). Study of the food relations in Cedar Bog Lake strongly suggests that *Chaoborus* larvae feed in part upon *Ceratium* and rotifers, and also upon benthic ciliates and ostracods. Plankton predators, in turn, are much preyed upon by small fishes. The synthesized organic substance of this species may be entirely lost to the metabolism of the lake by emergence of the adult midges. Dead larvae are usually quickly reconverted to dissolved nutrients by bacterial action.

The appelation plankton predator is also applied (with some hesitation) to the back-swimming bugs, *Plea striola* Fieber, *Buenoa margaritacea* Bueno and nymphs of *Notonecta* species, all of which occur among the pondweeds. These bugs subsist primarily upon the "pseudoplankton" entomostracans (Hungerford, 1919). Their relative scarcity and small size forces them to a minor role in the food cycle of most lakes.

The pondweeds, as primary producers of organic substance, are relatively more important in Cedar Bog Lake than in deeper, larger lakes. During two of the four years studied, the pondweeds (used here in the broadest sense of the term) produced more organic substance than did the phytoplankton. *Najas flexilis* (Willd.), together with *Potamogeton zosteriformis* Fernald and *P. panormitanus* Biv., was so abundant (except during 1938) as to form a submerged "meadow" covering more than half of the entire lake bottom.

Ceratophyllum demersum L. is usually interspersed with *Najas* in the shallower water near the lake margin. This pondweed "meadow" forms an abundant source of food for a great variety of browsing animals, as well as a locus of attachment for many sessile plants and animals. Several different food groups are thus dependent upon the submerged pondweeds. In late autumn the pondweeds die and party decompose, forming a thick nutritive layer of nascent ooze over a considerable part of the lake bottom. The decomposition of this ooze accounts to a considerable extent for the annual depletion of oxygen beneath the winter ice.

The **epiphytes** attached to the submerged pondweeds, including many kinds and varieties of bacteria, diatoms, green and blue-green algae, form an increasingly heavy coating over the pondweeds as summer progresses. Most conspicuous of these is *Gloeotrichia pisum* (Ag.); this species grows so rapidly that by midsummer the leaves and stems of *Potamogeton zosteriformis*, the species first affected, are thickly encased with the hemispherical thalli. During this period the dry weight of the epiphyte is considerably greater than that of the supporting pondweed. The trichomes of *Gloeotrichia*, incompletely decomposed on the lake bottom, are found in great numbers in the sediments of the lake.

Filamentous algae such as species of *Spirogyra* and *Oedogonium* are commonly associated with the pondweeds. During early summer these algae form dense masses which blanket the water surface near the margins. Certain colonial flagellates such as *Pandorina morum* Bory and *Eudorina elegans* Ehr. seemed to be more common among the pondweeds than in the open water zone.

The microfauna associated with the pondweeds includes many sessile, creeping and free-swimming herbivores. Rotifers, including such genera as *Diurella, Lecane, Euchlanis, Trichocerca* and *Platyias*, were abundant; entomostracans, including such cladoceran genera as *Pleuroxus* and *Chydorus*, and such ostracod genera as *Cypria* were usually common. These organisms, feeding on seston and to a lesser extent upon the nearby epiphytes, are preyed upon by certain carnivorous species of *Cyclops* (Naumann, 1923); both micro-predator and micro-prey are subject to intense predation by small fishes and other swimming predators.

The macrofauna, which portrays an almost infinite variety of food habits, has been classified according to "primary" dietary habits into browsers, benthic predators, plankton predators and swimming predators. The term **browser** is here roughly defined as an herbivorous or saprophagous animal which feeds primarily on its substrate. The distinction between plant browsers and ooze browsers does not appear to be justified; many species which are primarily herbivorous during the summer are saprophagous during the winter; others appear to feed indiscriminately upon both living and dead plant material.

Many **browsers** are associated primarily with living pondweeds. Prominent among these are several genera of pond snails, *Helisoma, Planorbula,*

Menetus, Gyraulus, Physa and *Amnicola;* these usually are found on living pondweeds, but also feed on epiphytes, ooze and even decomposing animal tissue (Wesenberg-Lund, 1939), depending upon predilection and availability. Although some specific food-differences have been observed, these genera are essentially similar in relation to the general food cycle. The common amphipod *Hyalella azteca* (Sauss.), which is primarily a browser on pondweed epiphytes (Jackson, 1912), occupies a food-cycle position essentially similar to that of the snails. A small species of the oligochaete *Nais*, possessing pigmented eye-spots, was often abundant among the pondweeds; according to Wesenberg-Lund (1939), *Nais* feeds primarily on epiphytic plants and certain members of the associated microfauna.

Several types of immature insects browse on the pondweeds and pondweed epiphytes. Such chironomid larvae as species of *Endochironomus, Tanytarsus* and *Cricotopus* (cf. Moore, 1915, p. 284) become particularly abundant at certain times of the year. Certain mayfly naiads of the subfamily *Baetinae* are often observed creeping and apparently browsing upon the pondweeds. Caddisfly larvae of such genera as *Phryganea, Limnophilus* and *Platyphylax* are found associated with the pondweeds; these larvae feed upon green plant tissue (cf. ibid.), although they may also eat ooze, depending upon which source of food is most convenient (Lloyd, 1921).

Browsers particularly abundant in *Spirogyra* masses include larvae of the ceratopogonid genera *Stilobezzia* and *Dasyhelea*, and species of the crawling water beetles, *Haliplus* and *Peltodytes*. The former were found only among *Spirogyra* masses, on which they feed, while the latter were also found among pondweeds and sometimes in the ooze. According to Hickman (1931) *Spirogyra* is the principal food of the larvae of these beetles, while the adults forage upon a wider variety of vegetation.

Browsers common during the summer months on both the pondweeds and the benthic ooze include naiads of the mayfly genus *Caenis*, larvae of th soldierfly genus *Odontomyia* and tadpoles of the leopard frog, *Rana pipiens* Schreber. *Caenis*, which is usually abundant in the pondweed zone of Cedar Bog Lake, is characteristic of the upper sublittoral zone of larger eutrophic lakes, as a "Pflanzendetritus bevorzugendes Tier" (Lundbeck, 1926, p. 168). The larvae of *Odontomyia*, often numerous among pondweeds near the lake margin, feed on pondweed epiphytes, entomostracans and nascent ooze (Malloch, 1917). Frog tadpoles, usually common near the lake margin, feed on filamentous algae and various constituents of the benthic ooze (cf. Morgan, 1930).

A group of browsers more strictly associated with the ooze in the pondweed zone consists of the water-boatmen *(Corixidae)*, the adult water scavenger beetles *(Hydrophilidae)* and the deerfly *(Chrysops)* larvae. The *Corixidae*, which are at times very numerous in the lush *Najas* "meadow" of Cedar Bog Lake, are primarily ooze browsers, sweeping the flocculent surface ooze into their mouths by means of their fore tarsi (Hungerford, 1919). These

small bugs are much parasitized by larval water mites, and are extensively preyed upon by various carnivorous insects. Hydrophilid beetles are represented in the lake by *Tropisternus*, *Enochrus* and *Berosus*, as well as other genera of smaller size. The adults of these beetles are primarily ooze browsers, but also eat dead animal tissue (Richmond, 1920). The larvae of *Berosus* are sluggish browsers (Wilson, 1923), in contrast to the (predatory) larvae of the other genera. *Chrysops* larvae, which occur rather commonly in the marginal ooze, are also (Johannsen, 1935) primarily ooze browsers.

The true ooze browsers of eutrophic lakes consist largely of midge larvae belonging to the genus *Chironomus*. In the marginal and pondweed areas of Cedar Bog Lake, *Chironomus lobiferus* Say is the most important species, living in crevices of sticks, inside the stems of aquatic plants, or in the absence of these, in reinforced U-shaped tubes in the ooze. The primary species in the more tenuous planktogenic ooze in the middle of the lake are *Chironomus plumosus* L. and *Chironomus decorus* Johannsen, which also live in reinforced tubes. The food of these three species is essentially similar, consisting largely of settled plankton, ooze-film organisms and flocculent particles of planktogenic ooze (cf. Richardson, 1921; Leathers, 1922).

Because of their abundance *Chironomus* larvae play an important role in the "intermediary metabolism" of the lake. Much of the benthic ooze passes at least once through their digestive tracts, as indicated by innumerable fecal balls in the unconsolidated deposits. The flow of water through the deep tubular burrows, set up by undulatory (respiratory?) movements of the larvae, serves to permit oxidation of the ooze to considerable depths by the action of aerobic bacteria, thus furnishing large amounts of released nutrient ions to the water above. *Chironomus* larvae are able to withstand extended periods of anaerobic conditions (Lindeman, 1942a). The seasonal distribution of the above species in Cedar Bog Lake is considered in detail in another paper (Lindeman, 1942b). They harbor considerable numbers of the large parasitic nematode, *Hydromermis* sp; by serving as a source of food for benthic and swimming predators, *Chironomus* larvae form an important link in the food cycle of the lake.

Less numerous ooze browsers in Cedar Bog Lake are the finger-nail clams, species of *Pisidium* and *Musculium*. The former were collected in the deeper areas during 1937 and 1938; numbers of the latter were found in marginal collections during 1939 and 1940. The slender worm leech, *Helobdella nepheloidea* (Graf), common in the marginal areas during 1937 and 1938, is also primarily an ooze browser (cf. J. P. Moore, 1912).

Microscopic ooze browsers, because of their periodic abundance, may often be as important to the food-cycle economy of the lake as are the macro-browsers. During the late autumn of 1939, for example, a tremendous fauna of *Chaoborus* is believed to have been maintained largely by the great masses of micro-browsers present at that time. The great majority of these browsers consists of ciliates, primarily *Frontonia leucas* Ehr. and *Loxodes rostrum* (O. F. M.). With the exception of a few protozoan and rotiferan predators, most

of these organisms are ooze browsers, feeding on tiny particles of ooze and probably obtaining much of their nutritive requirement from the benthic bacteria. Besides the ciliates are found such gastrotrichans as *Lepidoderma rhomboides* (Stokes) and several species of *Chaetonotus*, many small free-living nematodes, *Ilyocryptus* and smaller benthic cladoceran genera, the copepod genus *Canthocamptus*, and the ostracod genera *Candona* and *Cypria*. All of these organisms are primarily ooze browsers (cf. Wesenberg-Lund, 1939), and form a very interesting and taxonomically complex fauna. Unfortunately no attempt was made to evalute the role of micro-browsers in the food-cycle dynamics of the lake. This was due partly to the difficulties of counting such organisms in freshly taken ooze and partly to the belief that larger browsers, such as chironomid larvae, did not discriminate between the surface ooze and its contained microbiota. It now appears, however, that at least certain predators, such as *Chaoborus*, carefully discriminate between ooze and microfauna.

The **sediment-transporters** deserve particular mention, although the results of their ooze-browsing activities are not conspicuous in Cedar Bog Lake. The tubificid oligochaetes, *Limnodrilus* and *Tubifex*, live in tubes with their anterior ends deep in the ooze and their posterior ends waving about in the water just above. Alsterberg (1922) was the first to demonstrate that these worms suck in particles from the lower ends of their tubes and defecate the undigested remains at the ooze surface; he later (1924) described the trophic significance of their role as sediment-transporters in a paper which has been widely quoted. Wesenberg-Lund (1939), however, declares that it still remains to be demonstrated that the scraping together of particles from the ooze surface may not equally serve as a source of nutriment. Observations on tubificids in aquaria by the present author indicate that sediment-transportation does occur, and that with large populations of these worms, its effects may be considerable.

In summarizing the status of the many diversified browsers in the food cycle of Cedar Bog Lake, it should be re-emphasized that these organisms constitute the most important link between the synthesized organic matter produced by autotrophic plants and the higher predators of greatest economic importance to man. Within the broad limitations imposed by differential respiratory adaptations, the practical fish productivity of a lake seems to be directly correlated with the abundance of browsers.

The **benthic predator** sector of the food cycle contains several groups of secondary consumers related only in their predatory dependence on the browsers and the general inability to swim. Several types of predatory techniques are employed, varying from pursuit to ambush and allurement. The effect upon the prey may vary from engulfment to bloodsucking and temporary or permanent parasitism.

The most important creeping predators in the central portion of the lake are midge larvae. *Chironomus (Cryptochironomus) stylifera* Johannsen represents a carnivorous larval group of an otherwise herbivorous genus. The larvae of *Procladius culiciformis* (L.), *Tanypus stellatus* Coq., *Pentaneura*

sp., and *Anatopynia dyari* (Coq.) of the predatory (cf. Johannsen, 1937) subfamily *Tanypodinae* are also sporadically common. Predatory (cf. Thomsen, 1937) vermiform larvae of the *Palpomyia*-group of *Ceratopogonidae* are usually very abundant in the central part of the lake. Since these predatory larvae appear to feed primarily on browsing chironomid larvae, a large predatory population may greatly reduce the numbers of browsers. These predators are in turn subject, together with the remaining browsers, to extensive predation by the larger swimming predators.

The creeping predators of the pondweed beds consist primarily of leeches. The snail leeches, *Helobdella stagnalis* (L.), *Helobdella fusca* (Castle) and *Glossiphonia complanata* (L.), sporadically abundant in the lake, creep along the ooze surface and among the pondweeds; they feed by sucking the internal tissues from such snails, worms, insect larvae and other sluggish forms as cannot elude them (cf. Moore, 1912). As the name "snail leeches" implies, snails form the chief component of their diet. The turtle leeches, *Placobdella rugosa* (Verrill) and *Placobdella parasitica* (Say), appear to be alternately predatory and parasitic. They are often found as ectoparasites on the painted and snapping turtles, respectively, but they seem unable to swim and spend their free-living periods on the marginal bottom or among the pondweeds. Their predatory food habits (cf. Moore, 1912) are essentially the same as those of the snail leeches. The turtle leeches are thus seen to occupy at different times two quite different sectors of the food cycle. Since turtles are usually uncommon in the lake, these leeches are grouped with the snail leeches. Small leeches are extensively preyed upon by fishes and other swimming predators.

More sedentary benthic predators are the naiads or dragonflies and damselflies, which are often numerous in the marginal areas of the lake. The damselfly naiads are usually found in the tangled masses of pondweeds, where they prey upon such browsers as chironomid larvae and mayfly naiads, as well as upon entomostracans (Garman, 1917). The dragonfly naiads can be found half-buried in the ooze or supported on bits of aquatic vegetation; they lie in wait for the approach of smaller animals, which are impaled on the labial hooks by a quick thrust of the labium and drawn toward the crushing mandibles. Because of their size dragonfly naiads are the most "dominant" of the benthic predators; they are immune from the small fishes inhabiting the lake, and only the large swimming leeches are able to prey upon them.

A specialized group of small animals which are both predators and parasites are the water mites or *Hydracarina*. Considerable numbers of these animals are found in the pondweed beds; a species of *Limnesia* is found rather consistently in the ooze of the open water zone, and is able to withstand considerable periods of anaerobiosis. The larvae are ectoparasites on various aquatic insects; the adults feed as swimming predators on entomostracans and small insect larvae, although because of their small size they are preyed upon in turn by small fishes.

Before discussing the role of swimming predators in Cedar Bog Lake, we shall veer from our course to mention an obvious "side-chain" to the aquatic food cycle — the **neuston**, or surface-film organisms. The neuston has consid-

erable claim to being considered as a separate community in its own right. Autotrophic bacteria, unicellular algae and abundant masses of *Lemna* and *Spirodela*, covering the surface in quiet-water areas, act as the producers for the community; the animal consumers include both browsers and predators. The associated organisms of a *Lemna* community are charmingly described by Scotland (1934) in her short paper, "The Animals of the *Lemna* Association."

Animals extending beyond the limited areas of the "*Lemna* association" consist of certain protozoans and entomostracans suspended from the under side of the surface film; *Microvelia* species which feed on these (Hungerford, 1919), are present during the summer in considerable numbers. The larger predators, which "skate about" on the surface film and feed on terrestrial animals fallen into the water from the margin or the air above, include such genera as the water strider *Gerris*, the whirligig-beetle *Dineutes*, and the semi-aquatic spider *Dolomedes*. All of these forms may at times become rather abundant on the surface of the lake. All members of this surface-film community are subject to the action of swimming predators from below, which tends to incorporate the organic substance of this community into the larger food cycle of the lake.

The most conspicuous **swimming predators** in quantitative collections from the pondweed and marginal areas consist of the larger aquatic insects. Among these must be included the adult back-swimmer, *Notonecta* sp. (Hungerford, 1919), although the nymphal stages feed primarily as plankton predators. The adult *Notonecta* is a fierce predator, quite capable of attacking small fishes and other animals larger than itself. Other highly carnivorous animals in the pondweed areas are the water-tigers and the predacious diving beetles, larvae and adults, respectively, of the family *Dytiscidae*. The water-tigers have an amazingly insatiable appetite, possessing hollow piercing mandibles which enable them to suck the juices from their victims without loosening their initial hold. Mayfly and damselfly naiads, chironomid and smaller beetle larvae are choice prey for these creatures, but no aquatic animal may consider itself safe from the larger water-tigers—snails, tadpoles, frogs and even fishes all fall before their onslaughts (Wilson, 1923). The larvae of *Tropisternus* and other aquatic *Hydrophilidae* are similarly carnivorous. The adult *Dytiscidae*, represented in the lake by such genera as *Hydaticus*, *Coptotomus*, *Desmopachria* and *Rhantus*, are agile swimmers and strictly carnivorous. According to their size they eat dragonfly, damselfly and mayfly naiads, as well as aquatic hemipterans, chironomid larvae and snails (Wilson, 1923). All of these beetles must be considered as swimming predators.

A group of more sluggish swimming predators, definitely restricted to the dense pondweed masses near the lake margin, are represented by large bugs, including species of *Ranatra*, *Nepa*, *Lethocerus* and *Belostoma*. The former two, known as water-scorpions because of their long caudal breathing-tubes, spend most of their time in the tangles of *Najas* and *Ceratophyllum* waiting motionless for some unwary creature to come within reach; when this happens the raptorial fore legs quickly snatch the prey, and the nutritive fluids are

sucked from its body (Hungerford, 1919). *Lethocerus* and *Belostoma* are fierce predators, able to kill and devour even such large organisms as minnows and frogs (Needham, 1918), although their usual diet consists of smaller forms. No organisms in the lake except the turtles and muskrats are safe from these bugs. These four genera, together with the predatory beetles, compete for "animal dominance" in the marginal areas, since the small fishes present in the lake seem unable to prey upon them effectively. This "dominance" must, however, be shared with the swimming predatory leeches, which also function as the "end of the food-chain" in this part of the lake.

Another important group of swimming predators is composed of the swimming leeches, *Erpobdella punctata* (Leidy) and *Macrobdella decora* (Say), which are numerous during those years when fishes are few in numbers. These leeches are good swimmers and, although occasionally acting as scavengers, ordinarily prey upon worms and aquatic insects (Moore, 1912). *Erpobdella,* the more common genus, even attack small fishes and frogs; large quantities of ooze are often swallowed, but this is believed to be an unimportant factor in its diet. *Macrobdella,* the well-known blood-sucker, prefers to feed upon the blood of vertebrates plus whatever invertebrate forms it can capture. Frog eggs are often eaten, and the writer has observed the consumption of *Pimephales* eggs by this leech. Because of the versatility in food habits of these leeches, enabling them to fit into several carnivorous food-groups according to predilection and availability of food, it seems certain that they should be grouped with the fishes as very important swimming predators.

The major swimming predators of Cedar Bog Lake, the fishes, are of extreme importance in the food-cycle dynamics of the lake. During the course of this investigation four species, all small and of the type known as "forage fishes," were found in the lake: *Pimephales promelas* Raf., *Umbra limi* (Kirtl.), *Eucalia inconstans* (Kirtl.) and *Apomotis cyanellus* (Raf.). All of these species typically are found in small sluggish streams with marshy bottoms. Cedar Creek, into which the lake sporadically drains, is definitely of this type. The lake outlet follows a vague surface course through the bog forest, where tree roots and hummocks combine to conceal any continuous channel. Presumably the fishes are able to perceive a current, and since the maximum flow coincides with the spring spawning season, they must manage to follow its mile-long course by wriggling from pool to pool until they arrive at the lake itself.

The difficulties involved when one attempts to place an organism into a rigid "niche" of an arbitrary food cycle are particularly apparent in the case of certain fishes. The food habits appear to vary in different habitats; it may be that fishes have individual food preferences at different times, occasionally varying their usual diet (of chironomid larvae, for example, with pondweed fragments), just as terrestrial carnivores occasionally modify their usual diet with bits of grass.

The fat-headed minnow, *Pimephales promelas,* is a hardy species, very resistant to asphyxiation; it is not surprising to find it the most abundant fish

in the lake. The food of 3 young specimens 12-15 mm. in length was found to consist of mixed phytoplankton and zooplankton, the latter consisting of protozoans, rotifers and nauplii, but no adult copepods nor cladocerans. The food of 8 specimens 28-38 mm. in length was found to consist of filamentous algae and larger zooplankters. Two individuals 35-40 mm. in length were starved for a week and then placed in an aquarium containing submarginal Cedar Bog Lake ooze, to which a small mass of *Spirogyra* (abundant in the lake at that time) had been added, so that the resulting food conditions were believed to correspond to those existing in the lake. Two days later the fishes were removed and their food determined. No ooze was taken by the minnows in spite of their proximity to it; the food was almost wholly of animal origin and consisted of chironomid larvae, bryozoans *(Plumatella), Plea* and chironomid adults. A very small amount of algae (ca. 5%) was eaten, consisting of *Spirogyra* and *Oscillatoria*. From these food-habit data it was concluded that *Pimephales* changes its food preference with growth. The young individuals seem to be general plankton predators, while the adults, although they never quite renounce their vegetarianism, may be considered as swimming predators.

The five-spined stickleback, *Eucalia inconstans*, although never abundant, was found in the lake during three of the five years studied. This species, which has a short intestine typical of carnivores, was reported by Forbes and Richardson (1920), based on five specimens, to feed on filamentous algae, entomostracans and chironomid larvae, the algae making up 50% of the food. Two specimens from Cedar Bog Lake were found to have fed almost entirely on copepods and ostracods, as well as on a few smaller zooplankters. Thus these individuals seem to prey upon the microbenthic ooze-surface organisms as do such other plankton predators as Chaoborus larvae. Since *Eucalia* is also known to eat *Chaoborus* and chironomid larvae, it must be considered as a swimming predator.

The mud minnow, *Umbra limi*, the most mud-loving of our piscian fauna, was found very regularly in the lake; during 1938 it was the only species found. *Umbra* is reported by Forbes and Richardson (1920) to be largely vegetarian, with animals making up about one-fourth of its food. A study of 8 individuals from Cedar Bog Lake showed that more than 90% of the food taken was of animal origin. Chironomid larvae, corixids, small adult beetles, collembolans, water mites and many entomostracans made up most of its food. Because of the definitely carnivorous diet of the specimens examined, the author has no hesitation in considering *Umbra* as a swimming predator.

The green sunfish, *Apomotis cyanellus*, was rare in the lake, and present only during 1939 and 1940. Although this species is typical of small soft-bottomed streams, it seems rather surprising that it could have accomplished the "hedge-hopping" presumed necessary to traverse the bog forest area from Cedar Creek to the lake. This species, in common with other *Centrarchidae*, is definitely predatory. Young individuals feed on entomostracans; older ones on insects, small crustaceans and other fishes. It readily falls into the category of a swimming predator.

It should be emphasized that the fish population of Cedar Bog Lake is quite different from that of larger eutrophic lakes. In larger lakes the larger carnivorous fishes are able to prey on the smaller "forage fishes" as well as on any other of the subservient groups of the food-chain. In Cedar Bog Lake the devastating anaerobic period during winter stagnation necessitates new immigration each spring, so that the offspring of such large carnivorous fishes as might reach the lake cannot attain more than the first year of growth. As a result the fishes must share honors as "dominant animals" with the swimming leeches and those larger swimming insects which the fishes are unable to eat. The swimming predators of Cedar Bog Lake are thus seen to be secondary consumers rather than tertiary consumers as are the dominant fishes of larger lakes.

Although **air-breathing tetrapods** are not, strictly speaking, a part of the senescent lake community, many of them are intimately dependent on it for food. The leopard frog, *Rana pipiens* Schreber, is often common near the margin, preying upon snails, Hyalellae, worms and aquatic insects (Dickerson, 1906), which comprise substantial portions of its diet. The painted turtle, *Chrysemys picta bellii* (Gray), of which several individuals can usually be seen in the lake, makes up about $\frac{2}{3}$ of its diet from pondweeds. The remaining third is made up chiefly of aquatic insects, but also includes snails, Hyalellae, leeches and fishes (Lagler, 1940). Numerous ducks feed on such aquatic plants as may be found during the migration periods, and usually one or two pairs of teals nest on the lake during the summer. Kingfishers and bitterns, birds which feed on the aquatic fauna, have been occasionally observed, but are not believed to exert much influence on the food cycle of the lake as whole. During 1939 several pairs of muskrats *(Ondatra)* immigrated to the lake, and presumably consumed a considerable amount of aquatic vegetation (cf. Enders, 1932); these muskrats perished during the winter and have not since been replaced. The tetrapod predators are not numerous in Cedar Bog Lake and, from the point of view of the lake as a whole, do not seriously affect the purely aquatic aspect of the lake's ecology.

Heterotrophic bacteria are the primary agents, apart from the excretion of dissolved substances by higher organisms, in the regeneration of dissolved nutrients within a lake. Very few data have been published on this aspect of food-cycle dynamics, so that a few preliminary notes from Cedar Bog Lake material are noteworthy. A series of cultures of benthic ooze (XII-8-40), at three concentrations of ooze in standard culture water (cf. "Standard Methods for the Examination of Water and Sewage," 1936) at 20° C. for 5 days, showed an oxygen consumption of 4.7 mg/l of O_2 per 50 mg dry ooze. This represents the activity of aerobic bacteria. The activity of anaerobes in ooze from the same place (XI-15-39) is suggested by data taken from another manuscript (Lindeman, 1942a). Quantities of ooze representing approximately 30 times the concentration above were placed in blackened culture jars and kept under anaerobic conditions at constant temperatures of 0°, 5° and 10° C. for a maximum of 120 days. The increase in bicarbonate alkalinity was recalculated as increase in CO_2 (mg/l of CO_2) per 50 mg dry ooze

for direct comparison with the aerobic data given above. The recalculated values are:

	30 days	60 days	90 days	120 days
0°	.12	.31	.37	.42
5°	.09	.20	.21	.40
10°	.18	.32	.44	.51

Although such data may be criticized on several bases, these figures suggest that aerobic bacteria are many times as effective as anaerobes in regeneration of benthic nutrients; the accumulation of organic deposits in the profundal areas of eutrophic lakes also indicates that such is the case.

Regeneration of dissolved nutrients, at least in part, is absolutely essential to the functioning of any nutritive cycle. A certain amount of essential nutrient substance potentially may leave the lake from any sector of the primary food cycle. Drainage through the lake outlets during periods of high water may remove dissolved nutrients, phytoplankton and zooplankton. Emergence of adult stages of aquatic insects may remove living animal tissue from the browser, plankton predator, ooze predator and swimming predator food groups. Predation by tetrapods may permanently remove organic substance from the pondweed, browser and any or all of the predator groups mentioned above. Perhaps the most important loss of substance to the food cycle in this lake is by sedimentation on the lake bottom. Compensating for these losses, however, is the influx of a certain amount of dissolved nutrients from the surrounding drainage basin. Aside from these losses and additions, the aquatic food cycle is self-contained, again decomposing that organic substance to which it has given rise, and in a large measure regenerating from the organic ooze the nutrient salts essential for further phytosynthesis.

In brief recapitulation of trophic relationships, the autotrophic plants are the producers of organic substance in the lake; numerous animal groups play intricate, interrelated roles as primary, secondary and even tertiary consumers of this organic substance; heterotrophic bacteria act as decomposers of organic substance and, from another point of view, as regenerators of essential plant nutrients. Thus the food cycle revolves.

Quantitative Seasonal Dynamics

The study of seasonal changes in the metabolism of lakes requires comprehensive analyses of processes both directly and indirectly related to the food cycle. In the present study on the senescent Cedar Bog Lake, the author makes no claim for such comprehensive treatment. An attempt has been made, however, to determine simultaneous seasonal values for certain environmental conditions as well as for the biological populations.

The seasonal dynamics was studied by means of periodic surveys, covering the period from December 21, 1936, to March 28, 1941. Nearly 50 such survey trips were made, during which more than 40 series of plankton and water-chemistry samples, and 30 series of bottom samplings (338 Birge-Ekman dredge collections) were obtained. While most stress was placed on the fluctuations in bottom fauna, quantitative estimates of various other food groups and environmental conditions were made at the time of each survey.

Since fluctuations in certain of the environmental "factors" are reflected in the coincident biomass, it seems advisable to present the seasonal analysis of (1) water level variations correlated with climate and (2) fluctuations in chemical conditions, before considering the quantitative biological dynamics.

Water-Level Variations Correlated with Climate

The surface level has been so directly correlated with profound changes in the ecology of the lake that an accurate account of its fluctuations, together with those of the causative climatic factors, is highly desirable. The available data on mean monthly temperature, mean annual precipitation and mean monthly precipitation from nearby weather stations, as well as the surface level of Cedar Bog Lake, depth of winter ice and depth of free water in the center of the lake, are recorded in Fig. 3.

The mean annual duration of ice, shown as shaded blocks in the figure, was estimated from personal observations: in this region ice usually forms on small shallow lakes in mid-November and lasts until about April 1. Deviations from this arbitrary norm may be seen by the way in which the curve of mean monthly temperature intersects the block representing mean annual duration of ice. Thus, the spring of 1938 was abnormally warm, as was also the late autumn of 1939. The air temperature curve was plotted from the mean monthly values at Cambridge, Minnesota, about 15 miles north of Cedar Bog Lake.

Mean monthly variations in aqueous precipitation at Cambridge, Minnesota, are indicated by the solid line representing "precipitation." Extreme deviations from the mean annual curve (based on the 37-year records of precipitation at Milaca, Minnesota, about 35 miles from the lake) were found at all seasons of the year. It should be noted that in general the greatest amount of precipitation occurs during the warmest part of the year.

Measurements of water level fluctuations in the lake are indicated by small circles along the curve representing surface level. The records for 1936 were established by survey from the upland (Buell, 1941), while the intervening fluctuations for 1936 were estimated, as shown by the broken line. All levels with lettered vertical ordinates indicate the maximum depths of water and of ice on successive dates when bottom-fauna collections were made. Undulations in the curve reflect indirect evidence that the lake had accordingly varied during the intervals between visits.

Comparison of the surface level curve with the mean monthly precipitation curve indicates a definite relationship; in spite of marked irregularities in precipitation, differential seasonal evaporation and the damming effects of the surrounding peat, a simple correlation coefficient of .409 was obtained for the two curves. The summer of 1936 was extremely dry, with the result that the lake level dropped more than one-half meter, exposing considerable sub-marginal ooze; vernal precipitation in 1937 greatly raised the lake level, serotinal drouth caused a decline, and autumnal precipitation produced another rise.

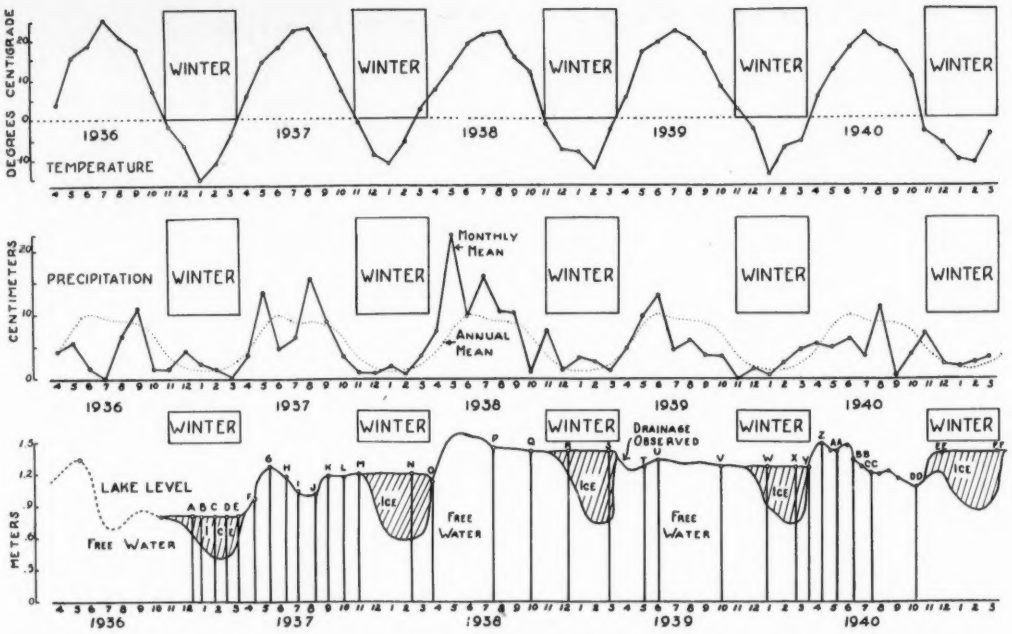

Fig. 3. Correlation of temperature and precipitation with the water level of Cedar Bog Lake.

Heavy precipitation throughout 1938 produced very high levels with theoretical drainage, although none could be observed on July 30. Buell (1941) has shown that the level of the entire bog forest fluctuates directly with precipitation, and that the forest is, in a manner of speaking, floating! Thus perhaps the lake outlet area floated up to a level at which surface water did not *flow*, but rather slowly *seeped* into the Cedar Creek drainage from adjoining portions of the bog. A similar damming effect of peat on lake drainage was noted by Lewis and Cocke (1929).

A peculiar phenomenon was observed in the spring of 1939; although precipitation was normal and melting snow should have greatly raised the water level, just the opposite event occurred, and the level *dropped* some decimeters. Fortunately for our records, Dr. W. H. Crone observed in early April that a considerable drainage stream "6 inches deep and quite wide" was flowing from the southwest portion of the lake across the bog forest toward Cedar Creek. The lake was almost free of ice at that time but the forest peat, at depths of about 1 to 4 decimeters, was still frozen. The hypothesis is proposed that the surface waters of the lake and surrounding mat quickly drained in response to warm weather before the forest peat could thaw out sufficiently to float up and impede the drainage.

The data summarized in Fig. 3 thus indicate that the water level of Cedar Bog Lake is determined primarily by the aqueous precipitation. The surounding forest peat seems to exert a damming effect upon drainage from the lake.

Seasonal Fluctuations in Chemical Conditions

The chemistry of the water is so intimately related to the metabolic food cycle of the lake that seasonal fluctuations in dissolved substances often can be used to evaluate the intensity of biological processes. Field analyses of carbon dioxide, total alkalinity, pH and dissolved oxygen (according to the techniques described in "Standard Methods for the Examination of Water and Sewage," 8th ed.) were made during each survey visit to the lake, as shown in Fig. 4. It should be emphasized that the indicated lines in Fig. 4 merely show changes for consecutive survey dates and hence give no indication of the duration of a particular type of chemical conditions.

Dissolved oxygen in the center of the lake varied from 150% saturation on sunny midsummer afternoons to 0% in late winter. The exact duration of this winter oxygen-free period was determined only for the winter of 1939-40, when anaerobic conditions prevailed for 50 days (cf. Lindeman, 1942a). Reciprocal correlations between the summer concentrations of dissolved oxygen and of hydrogen ions, carbon dioxide acidity and total alkalinity (Fig. 4) are rather striking.

Carbon dioxide, produced largely from the decomposition of organic substances by bacteria and by respiration, combines readily with the salts of calcium and magnesium to be temporarily "stored" as bicarbonate dissolved

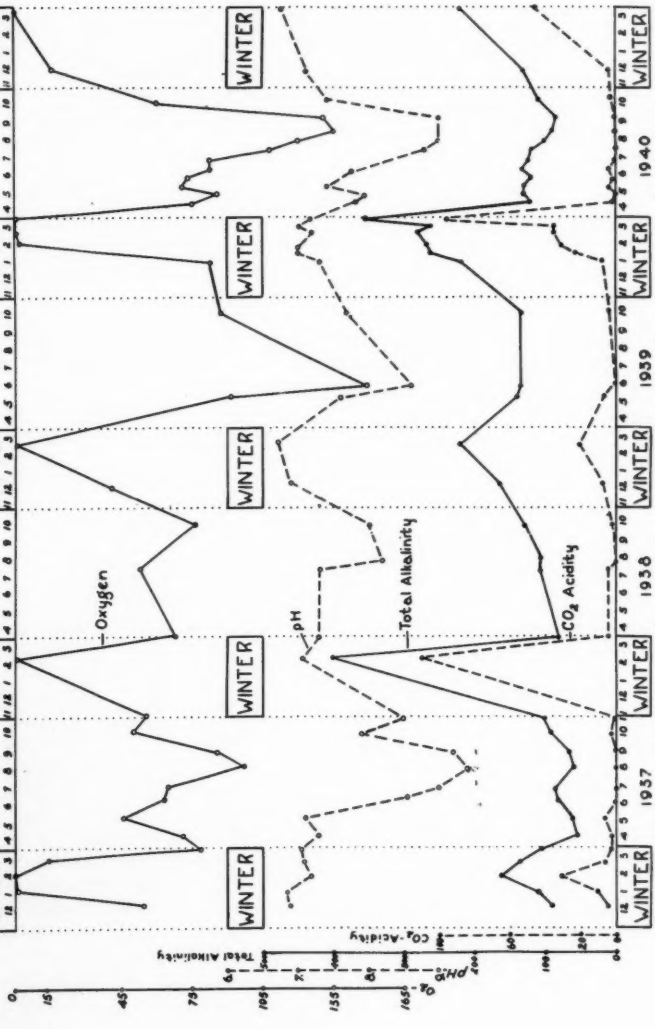

Fig. 4. Seasonal variations in dissolved oxygen, ph, total alkalinity and carbon dioxide in Cedar Bog Lake.

in the water, or more permanently stored as monocarbonate (marl) in the benthic ooze. Tests on the benthic ooze (IX-1-40) indicated a total alkalinity "reserve" of marl representing more than 1 gram per liter (as $CaCO_3$). The hydrogen ion concentration is largely a reflection of the equilibrium ratios existing between dissolved carbon dioxide and bicarbonate or between bicarbonate and monocarbonate, together with small amounts of other ionized substances. During winter stagnation the more soluble bicarbonate increases (as does carbon dioxide), so that the total alkalinity is raised three- or four-fold over its summer minimum. To obtain such extremes the light necessary for phytosynthesis must be effectively shut out by snow or granular ice. In midsummer carbon dioxide is "extracted" from the bicarbonate by the plants for photosynthesis, monocarbonate is precipitated from the warm lake water, the pH may rise as high as 9.4, and total alkalinity of the water is greatly reduced. Under such conditions the water is often supersaturated with oxygen, a product of photosynthesis.

The amount of carbonates and bicarbonates in a lake is limited, not by the ever-present carbon dioxide, but by the supply of calcium, magnesium and manganese. Total alkalinity is thus an index of these dissolved alkaline-earth metals. Analyses of the lake water for various seasons of the year indicated that the calcium content varied from 31 to 92 mg/l, while the magnesium content varied from 7 to 17 mg/l; manganese, present in relatively minute quantities, is included with the above magnesium values. Adding these together gives alkaline earth values ranging from 38 to 107 mg/l, figures which correlate very well with the total alkalinity values for corresponding dates, expressed in terms of the metals rather than as $CaCO_3$. Such concentrations of these metals, rather high for lakes in general, are due to leaching from the porous lime-containing soils of the surrounding region.

Iron, dissolved and suspended, is very abundant in the lake water. During winter stagnation ferrous salts are dissolved in considerable quantities; an analysis of water taken March 4, 1939, showed an iron content of 18-20 mg/l, as contrasted with a summer content of 0.2 mg/l. Reductive processes, initiated after the dissolved oxygen has been depleted, convert much benthic and suspended ferric iron to the ferrous state, which is very soluble in the carbon dioxide-laden, oxygenless water (Hutchinson, 1941). Samples collected after the onset of winter stagnation are bluish-black in color, reminding one of very dilute ink. If such samples are exposed to the air, the color of the water gradually changes to a brilliant ochre hue, while transparency becomes so greatly reduced (from ca. 50 to ca. 600 U.S.G.S. units) that one cannot see through it for more than a few centimeters. The ferrous ions are converted to insoluble ferric compounds (Einsele, 1936), which precipitate and are perhaps adsorbed upon some of the abundant dissolved organic substances to form the ochre-colored colloids. Since ferric phosphate may be precipitated in this manner, Hutchinson (1941) has emphasized that this process may play an important role in inhibiting the regeneration of phosphates from the benthic ooze.

Biological Food-Cycle Dynamics

Quantitative seasonal studies on lake biology have seldom emphasized the inter-relationships of various sectors of the primary food cycle. Such studies have been limited largely to the study of plankton or bottom fauna as a single unit without attempting either (1) to correlate the seasonal changes of the organisms studied with simultaneous changes in sectors of the food cycle other than water chemistry, or (2) to differentiate predators from prey. A partial exception to the first of these generalizations is represented by the correlations on Lake Mendota of Juday (1940), which, however, are not based on simultaneously collected data. A partial exception to the second generalization is represented by the analyses of Deevey (1942) of the bottom fauna of Linsley Pond, Connecticut.

The bottom biota of Cedar Bog Lake was sampled by means of the conventional Birge-Ekman dredge (15 x 15 cm.), modified to the tenuous ooze of Cedar Bog Lake by soldering a copper screen (40 meshes per inch, the same mesh size used for sifting) to the top of the dredge chamber. The sampler thus actually encompassed a vertical column from the surface of the water to a depth of at least 20 cm. in the bottom ooze. The samples were usually sifted in a wire-bottomed sieve immediately after collection, to remove all particles less than 0.5 mm. in diameter. The remaining coarse debris, including the biota, was placed in a glass jar, labeled, and preserved for examination in the laboratory. During the early part of this work 4 samples were collected in the open water zone, 4 in the pondweed zone, and 8 in the marginal zone. During 1940, 5 samples were taken from the open water and 5 from the pondweed zone, each sample being kept separate to permit statistical treatment of distributional data. During the winter months the marginal areas were frozen solid, so that samplings could be made only in the deeper zones.

Laboratory analysis of the bottom samples required the careful separation of organisms from the coarse detritus. This proved to be a laborious and time-consuming task, particularly in the marginal samples, because of the abundance of detritus on the lake bottom. The sorted organisms were identified, measured, counted and weighed. The weighing technique for each sample consisted of placing all the organisms of a single species in a small bolting-silk bag, centrifuging them in the bag for 3 minutes at 800 rpm to remove surface moisture, and then weighing them on a sensitive torsion balance. The resultant *moist* (centrifuged) weight is used as the basis, unless otherwise specified, of all weights mentioned in this paper. Conversion factors to dry weight for certain organisms are as follows:

Hydaticus	3.7	Caenis	5.6
Tropisternus	4.8	Chironomus	5.0-6.0
Palpomyia	5.3	Chaoborus	12.0-16.0
Hyalella	5.5		

It will be seen from these values that organisms possessing the greatest amount of chitin (*Hydaticus* and *Tropisternus* adults) are given less weight value than those possessing the least chitin *(Chaoborus)*. This is as it should be, for chitin is quite indigestible. From the trophic point of view, since dry weight values for insects as food are quite misleading, the moist weight values are believed to be based upon a more useful standard. The centrifuging technique has the added advantages of rapidity of measurement and of non-injury to the specimens, which may then be retained for other studies.

Field collections of net plankton were made by pouring approximately 100 liters of water through a No. 25 bolting-silk net; these samples, taken from three areas of the lake, were immediately preserved with formalin. Usually at the same time, quart samples of water from each station were preserved for the evaluation of nannoplankton.

Laboratory analysis of the net plankton consisted of comparing its quality and quantity (settled volume) with similar plankton samples from sources other than Cedar Bog Lake. The plankton of these other samples had been measured for quality and volume of settled organisms; then these were centrifuged for 3 minutes at 800 rpm, to remove surface moisture, and weighed on a sensitive torsion balance. From a series of such analyses conducted on miscellaneous samples of diverse species composition, factors were obtained for interpolating the settled volume of Cedar Bog Lake plankton, of known composition, into the appropriate centrifuged weights per unit volume. Although this round-about procedure was doubtless less accurate than centrifuged weights obtained directly from the quantitative plankton samples, the potential errors involved were deemed insignificant in comparison with the seasonal variation found. More important, this technique avoided the destruction of quantitative seasonal samples so valuable for future taxonomic and cyclomorphic studies. In small lakes containing abundant macrophytes, plankton often varied considerably in quantity from one part of the lake to another, requiring considerable subjective discrimination in estimating "true" values. Furthermore, the net samples often contain considerable floating debris. During microscopic analysis the percentage and quality of zooplankton, net phytoplankton and debris were estimated for each sample, and calculated in terms of moist weight. Analysis of the nannoplankton samples showed that while practically all of the zooplankton was retained by the net, often more than 90% of the phytoplankton consisted of minute nannoplankters which were not retained. The calculated populations of both nannoplankters and net phytoplankters are shown in Tables 1 and 2.

TABLE 1.—Food-Group Populations in Cedar Bog Lake, as gm/m², moist weight.

Series	Date	Swimming Predators	Benthic Predators	Browsers	Plankton Predators	Zooplankton	Net Phytoplankton	Nannoplankton	Pondweeds
A	XII-21-36*	....	4.60	50.20	0.03	0.00	0.02	1.0	0.0
B	I-18-37*	1.00	2.06	19.03	0.35	0.00	0.00	0.0	0.0
C	II-14-37*	....	2.85	35.64	0.70	0.00	0.00	0.0	0.0
D	III-8-37*	8.39	1.96	51.02	0.25	0.00	0.01	0.01	0.0
E	III-29-37*	4.36	3.03	52.90	0.58	0.01	0.04	0.01	0.0
F	IV-26-37	0.38	1.81	23.14	0.61	0.03	0.06	1.0	0.0
G	V-25-37	0.28	1.08	18.68	0.15	0.70	0.00	3.0	6.0
H	VI-26-37	0.81	1.26	3.38	0.01	0.10	0.10	1.9	150.0
I	VII-16-37	1.81	0.63	1.94	0.15	0.58	0.20	3.8	800.0
J	VIII-20-37	2.59	0.41	2.08	0.31	1.10	0.37	....	1800.0
K	IX-15-37	2.58	0.35	1.35	0.56	10.18	0.73	19.3	600.0
L	X-17-37	3.29	0.15	1.32	0.64	6.00	0.00	9.0	3.0
M	XI-13-37	3.63	0.15	1.03	0.31	2.52	0.03	15.0	0.0
N	II-26-38	0.01	0.05	0.54	0.27	0.00	0.00	0.0	0.0
O	IV-3-38	0.69	0.25	1.18	0.76	0.29	0.01	0.04	0.0
P	VII-30-38	0.07	0.02	1.55	0.37	0.69	1.38	0.6	250.0
Pa	VIII-15-38	....	....	....	....	2.16	19.40	0.6	300.0
Q	X-16-38	0.58	1.64	4.24	7.25	1.64	0.55	19.5	2.0
R	XII-22-38	±0.65	1.99	1.45	3.36	1.75	0.21	21.8	0.0
S	III-4-39	0.01	1.00	3.54	3.32	0.01	0.00	0.01	0.0
T	V-23-39	0.15	0.38	1.11	2.94	4.04	1.16	4.0	75.0
U	VI-15-39	0.11	0.30	0.84	1.80	2.45	46.55	0.5	200.0
Ua	IX-1-39	....	....	....	....	....	....	....	1000.0
V	X-15-39	2.63	0.71	3.56	26.27	1.22	0.16	6.8	3.0
W	I-13-40	2.50	0.44	14.82	22.95	2.00	0.43	7.5	0.0
Wa	I-31-40	....	....	....	....	2.12	0.00	3.0	0.0
Wb	II-7-40	....	....	....	....	1.17	0.07	0.03	0.0
X	III-3-40	0.00	0.77	16.93	±25.00	0.31	0.00	0.0	0.0
Y	III-30-40	....	....	....	....	0.01	0.00	0.0	0.0
Z	IV-28-40	0.48	0.79	7.91	18.76	1.21	0.01	10.0	1.0
Za	V-11-40	....	....	....	....	1.13	0.01	....	....
AA	V-26-40	0.13	0.90	2.69	22.05	2.59	0.11	2.4	50.0
AAa	VI-9-40	....	....	....	....	1.54	1.23	....	....
BB	VI-24-40	0.30	0.89	12.97	8.65	0.57	0.95	1.0	400.0
BBa	VII-7-40	....	....	....	....	0.71	2.73	....	....
CC	VII-27-40	1.20	1.09	16.86	0.97	1.20	23.70	0.3	1500.0
CCa	VIII-12-40	....	....	....	....	0.51	0.70	....	1800.0
CCb	IX-1-40	....	....	....	....	0.29	1.45	1.5	2000.0
CCc	IX-22-40	....	....	....	....	1.49	0.62	2.4	....
DD	X-20-40	3.00	1.54	1.96	3.02	0.26	0.06	....	5.0
EE	XII-8-40	3.25	3.60	1.50	3.70	0.40	9.00	3.0	0.0
FF	III-28-41	0.00	0.67	0.20	3.78	0.00	0.00	0.0	0.0

* Samplings inadequate, only 4 Ekmans taken on each date.

TABLE 2.—Food-Group Populations in Cedar Bog Lake, as cal/cm².

Series	Date	Swimming Predators	Benthic Predators	Browsers	Plankton Predators	Zoo plankton	Net Phyto-plankton	Nanno-plankton	Pond-weeds
A	XII-21-36*	....	0.46	4.18	0.00	0.00	0.00	0.06	0.00
B	I-18-37*	0.12	0.21	1.58	0.02	0.00	0.00	0.00	0.00
C	II-14-37*	....	0.28	2.97	0.03	0.00	0.00	0.00	0.00
D	III-8-37*	1.01	0.20	4.25	0.01	0.00	0.00	0.00	0.00
E	III-29-37*	0.52	0.30	4.32	0.03	0.00	0.01	0.00	0.00
F	IV-26-37	0.05	0.18	1.93	0.03	0.01	0.01	0.07	0.00
G	V-25-37	0.03	0.11	1.56	0.01	0.10	0.00	0.19	0.21
H	VI-26-37	0.10	0.13	0.28	0.00	0.01	0.01	0.12	5.25
I	VII-16-37	0.22	0.06	0.16	0.01	0.09	0.01	0.25	28.00
J	VIII-20-37	0.31	0.04	0.17	0.01	0.16	0.02	....	63.00
K	IX-15-37	0.31	0.03	0.12	0.02	1.48	0.05	1.25	21.00
L	X-17-37	0.40	0.02	0.12	0.03	0.87	0.00	0.59	0.10
M	XI-13-37	0.43	0.02	0.08	0.01	0.37	0.00	0.97	0.00
N	II-26-38	0.00	0.01	0.04	0.00	0.00	0.00	0.00	0.00
O	IV-3-38	0.08	0.03	0.10	0.03	0.04	0.00	0.00	0.00
P	VII-30-38	0.01	0.00	0.13	0.02	0.10	0.08	0.04	8.75
Pa	VIII-15-38	....	....	....	....	0.31	1.22	0.04	10.50
Q	X-16-38	0.07	0.16	0.35	0.32	0.24	0.03	1.27	0.06
R	XII-22-38	±0.08	0.20	0.12	0.15	0.25	0.01	1.41	0.00
S	III-4-39	0.00	0.10	0.30	0.15	0.00	0.00	0.00	0.00
T	V-23-39	0.02	0.04	0.09	0.13	0.59	0.07	0.26	2.62
U	VI-15-39	0.01	0.03	0.07	0.08	0.37	2.94	0.03	7.00
Ua	IX-1-39	....	....	....	....	....	....	....	35.00
V	X-15-39	0.32	0.07	0.30	1.15	0.18	0.01	0.44	0.10
W	I-13-40	0.30	0.04	1.23	1.01	0.29	0.02	0.49	0.00
Wa	I-31-40	....	....	....	....	0.31	0.00	0.20	0.00
Wb	II-7-40	....	....	....	....	0.17	0.01	0.00	0.00
X	III-3-40	0.00	0.08	1.41	±1.10	0.04	0.00	0.00	0.00
Y	III-30-40	....	....	....	....	0.00	0.00	0.00	0.00
Z	IV-28-40	0.06	0.08	0.66	0.82	0.18	0.00	0.65	0.03
Za	V-11-40	....	....	....	....	0.16	0.00	....	....
AA	V-26-40	0.02	0.09	0.22	0.97	0.37	0.01	0.16	1.75
AAa	VI-9-40	....	....	....	....	0.22	0.07	....	....
BB	VI-24-40	0.04	0.09	1.08	0.38	0.08	0.06	0.06	14.00
BBa	VII-7-40	....	....	....	....	0.10	0.17	....	....
CC	VII-27-40	0.14	0.11	1.40	0.04	0.17	1.50	0.02	52.50
CCa	VIII-12-40	....	....	....	....	0.07	0.04	....	63.00
CCb	IX-1-40	....	....	....	....	0.04	0.09	0.10	70.00
CCc	IX-22-40	....	....	....	....	0.22	0.04	0.16	....
DD	X-20-40	0.36	0.15	0.16	0.14	0.03	0.01	....	0.17
EE	XII-8-40	0.39	0.36	0.12	0.16	0.06	0.57	0.20	0.00
FF	III-28-41	0.00	0.07	0.02	0.16	0.00	0.00	0.00	0.00

* Benthic samplings inadequate; only 4 Ekmans taken on each date.

Seasonal fluctuations and inter-relationships of the primary food groups were analyzed in the following manner. Each species or genus was grouped according to food habits, as previously described, into the appropriate unit of the primary food cycle of the lake (Fig. 1). The resulting values, together with those obtained for the plankton, permitted the assemblage of seasonal weights for the following groups: (1) browsers, (2) benthic predators, (3) plankton predators, (4) zooplankters and (5) phytoplankters. Data for (6) pondweeds were based largely on estimates for the season, and include the weight of the epiphytic alga, *Gloeotrichia*. Fair estimates of (7) swimming predators were also obtained, since each year's fish production could be observed following suffocation during winter stagnation. The remaining units of the food cycle, unfortunately, were not similarly evaluated: no persistent attempt was made to analyze dissolved nutrients, bacterial activity or the annual increment of benthic ooze. The seasonal values for the seven food groups listed above are shown as gm/m^2, moist weight, in Table 1, and as calories/cm^2 in Table 2.

The conversion of weight values to calorific values is highly desirable for evaluating the relative nutritive content of various food groups. Thanks to the chemical analyses of many types of aquatic organisms by Birge and Juday (1922), the generally accepted bomb-calorimetry values for carbohydrate (4100 calories per gram), protein (5650 calories per gram) and fat (9450 calories per gram), as used by Juday (1940), can be utilized for the conversion. This method has certain inherent errors, since the organic composition of organisms changes with growth and nutrition, and since the bomb-calorimeter values do not indicate the extent of utilization of the food by the consuming organisms. It is, however, the most satisfactory method known for dealing with food conversions. The generalized factors for the conversion of food-group populations values from grams per square meter (dry weights and centrifuged weights) to calories per square centimeter are as indicated in Table 3.

TABLE 3.—Factors for the conversion of food-group weight values (gm/m^2) to food values (cal/cm^2).

Food-Group	*From Dry Weight*	*From Moist Weight*
Nannoplankton	.2610	.0652
Net Phytoplankton	.2525	.0631
Pondweeds	.3500	.0350
Zooplankton	.5800	.1450
Plankton Predators	.5330	.0440
Browsers	.5000	.0833
Benthic Predators	.5000	.1000
Swimming Predators	.6000	.1200

A more graphic presentation of the seasonal relationships of these food-group values is shown in Fig. 5, in which the calorific values of each group*

* Pondweed values are diagrammed as only 1/13 of the actual values to keep them within the confines of the chart.

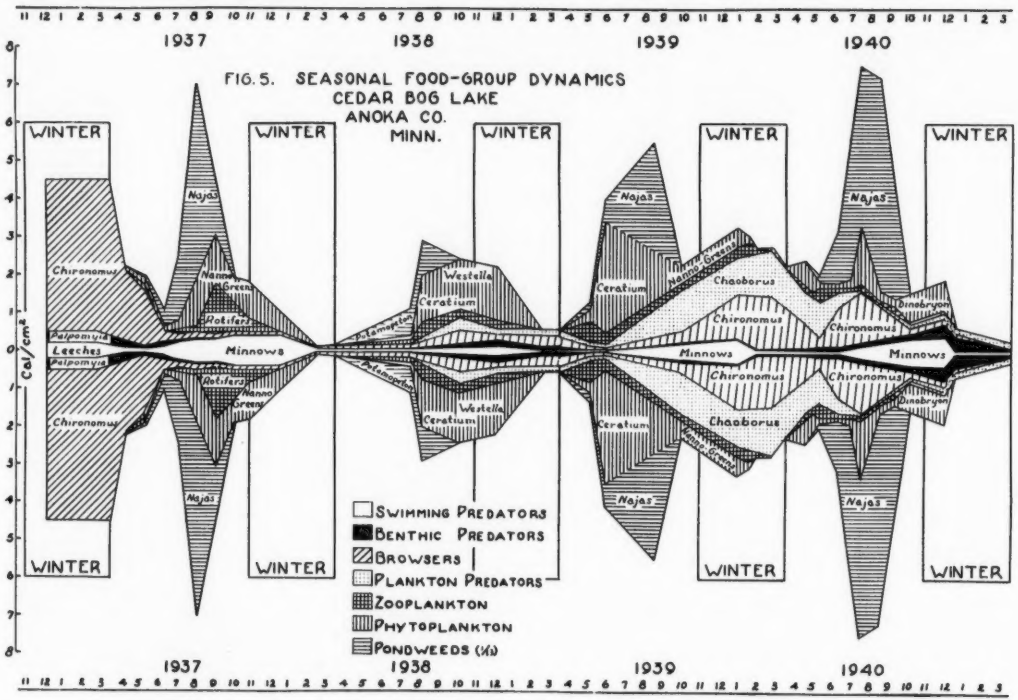

FIG. 5. SEASONAL FOOD-GROUP DYNAMICS
CEDAR BOG LAKE
ANOKA CO.
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are plotted successively in both directions from a central axis to emphasize the relationships of the groups to each other. The figure may be visualized as a sort of "sagittal section" through a cylindrical diagram. The duration of winter ice cover is indicated by the blocked areas labeled "ice."

Interpretation of the changing relationships of these food groups requires the careful consideration of simultaneous changes in water chemistry and climatic conditions, particularly the water level of the lake. The corresponding seasonal changes in climate, lake level and water chemistry are shown in Figs. 3 and 4.

The seasonal surveys were begun in the fall of 1936, following a summer of excessive drouth. The lake level was then lower than at any subsequent time during the period of this survey. No fishes were present in the lake during 1936, presumably because adults had been unable to immigrate during the preceding spring. The swimming predators were composed very largely of leeches, *Erpobdella punctata* being very abundant. *Palpomyia* larvae predominated among the benthic predators. Ooze browsers, composed very largely of *Chironomus lobiferus* larvae, were enormously abundant; pondweed beds had apparently covered most of the lake bottom during the summer, so that this pondweed-associated species could extend its range over the entire lake bottom. Plankton and plankton predators were very scanty during the winter.

Accompanying the spring thaw and heavy vernal precipitation of 1937 was a tremendous influx of water, actually doubling the volume of water in the lake. Some drainage must also have occurred through the bog forest peat west of the lake, as adults of *Pimephales, Eucalia* and *Umbra* were able to immigrate from Cedar Creek. Emergence of *Palpomyia* adults greatly reduced the benthic predators during early summer, although considerable numbers of creeping leeches were present. Emergance of *Chironomus* adults similarly reduced the browsers, although a tremendous May population of *Tanytarsus* tended to compensate this effect on the chart (Fig. 5). Plankton predators *(Chaoborus)* remained very scanty throughout this year. A slight bloom of the dinoflagellate *Ceratium* in May was followed later in the summer by a tremendous bloom of nannoplankters, primarily *Scenedesmus,* accompanied by a corresponding increase in the planktonic rotifers, particularly *Keratella.* As summer progressed an immense mass of *Najas* developed in the pondweed zone, estimated to average nearly 500 plants per square meter; these pondweeds became increasingly covered with epiphytic *Gloeotrichia* as the plants reached vegetative maturity.

Myriads of immature *Pimephales,* offspring of the spring immigrants, became increasingly predacious as summer progressed. Correspondingly, though perhaps not relatedly, the population of insect larvae changed completely from that of the preceding year. Almost no larvae of *Chironomus lobiferus* and *Palpomyia* could be found; *Chironomus plumosus* larvae were completely replaced by those of the smaller species, *Chironomus decorus.* During the winter following 1937 anaerobiosis was severe and prolonged, killing all of the fishes, the plankters and much of the benthos. On Feb. 26, species of the

following genera of organisms were still alive: *Chironomus (decorus* and *lobiferus), Procladius, Palpomyia, Chaoborus, Limnesia, Cypria* (?) and *Tubifex.*

In the spring of 1938, although the water level became very high, there was little surface drainage through the bog forest, probably due to differential thawing of the lake and the bog forest peat. Consequently, little new immigration of fishes occurred, so that, since the previous year's crop had all suffocated during the winter, the swimming predators consisted mostly of leeches. *Macrobdella* and *Erpobdella* were the most abundant swimming predators during 1938. The lake community had remarkably changed from its appearance in 1937. The tremendous *Najas* meadows of the former season were almost entirely gone, their photosynthetic function being only fractionally replaced by a sparse stand of *Potamogeton zosteriformis.* Total production of organic substance in the lake was thus strikingly reduced. During the early summer, predators, browsers and plankton remained at a low ebb. Between July 30 and August 15, however, a fifteen-fold increase in *Ceratium* transformed the entire aspect of the lake; whereas the water had previously appeared dark and blackish, it became "pea-soup green" from the contained dinoflagellates. The rotifer fauna also increased during this period, though not so phenomenally as the *Ceratium.*

Autumnal collections in 1938 indicated increasing populations of swimming predators (leeches), benthic predators *(Palpomyia)* and miscellaneous browsers, as well as a tremendous increase in the plankton predator, *Chaoborus.* While no experimental proof is at hand, it seems quite probable that the increased dinoflagellate supply aided in the population rise of this plankton predator. As the phytoplankton changed from *Ceratium* into the fall nannoplankton blooms of *Westella* and *Scenedesmus* (which was this year unaccompanied by a rotifer maximum), the *Chaoborus* population declined. Although populations disappeared rather abruptly with the onset of winter anaerobiosis, *Chaoborus* was able to maintain itself (on benthic ciliates?) until spring.

In the spring of 1939, as mentioned in the previous discussion of water levels, a small but definite stream of water was observed flowing through the bog forest from the lake toward Cedar Creek. A considerable number of adult minnows, and a few green sunfishes, were thus able to reach the bog lake. A distinct spring maximum of nannoplankters and zooplankters *(Keratella)* was noted (for the first time in the course of this survey) in May. Between May 23 and June 15 occurred another phenomenal (nearly fifty-fold) increase in *Ceratium,* which gave the water an even more striking "pea-soup" appearance than it had during the previous summer. It is further noteworthy that the "bloom" occurred fully two months earlier than in the previous year. Another striking difference from the previous summer was the reappearance of extensive *Najas* beds in the pondweed zone, although these were estimated to be only about $\frac{2}{3}$ as abundant as during 1937.

By autumn the immense *Ceratium* population had declined to near extinc-

tion, but an equally immense predatory *Chaoborus* population suggested at least one reason for its decline. Nannoplankters *(Scenedesmus* and *Westella)* attained an autumnal maximum which during this year was again unaccompanied by a rise in planktonic rotifers, these latter possibly also influenced by the *Chaoborus* hordes. Great numbers of *Chironomus* larvae appeared in October, this time with *plumosus* predominating, accompanied by great numbers of *decorus* and *lobiferus;* all grew very rapidly during the early winter. These, together with the *Chaoborus* larvae, showed a high survival of the 50 days of winter anaerobiosis. Surprisingly enough, the fishes, whose predatory capacities were increasing throughout the summer and autumn, seemed quite unable to keep these tremendous larval populations under control.

The effects of winter anaerobiosis during this winter were very carefully studied and compared with anaerobic simulation cultures kept at controlled temperatures. Although the details of this study appear in another paper (Lindeman, 1942a), the benthic larvae were found able, with considerable mortality to be sure, to survive at least 120 days of continuous anaerobiosis at 0° and 5° C., but could scarcely survive this duration at 10°. Comparisons made with changes in the lake fauna during its 50 days of anaerobiosis indicated that the natural populations in the lake declined more rapidly than did those in the simulation cultures.

In the spring of 1940, although surface drainage could not be observed, the lake level was very high and adult fishes were again able to immigrate to the lake. Emergence of *Chironomus decorus,* followed later by *lobiferus* and *plumosus,* greatly reduced the early summer population of browsers. A spring nannoplankton bloom of *Trachelomonas, Fragilaria* and *Euglena* was belatedly followed by an increase in rotifers. The large population of overwintered *Chaoborus* larvae was slightly augmented by a new brood in May, but gradually declined to a small minimum in late July.

The 1940 bloom of *Ceratium,* less conspicuous than in the two preceding years, occurred in July. Self-evident on the seasonal chart is the prolific summer crop of *Najas,* fully as abundant as that of 1937, and equally beset in midsummer with masses of epiphytic *Gloeotrichia.* The autumnal nannoplankton bloom of 1940, unaccompanied by a zooplankton bloom, was composed almost exclusively of *Dinobryon.* During midsummer a second generation of *Chironomus plumosus* reached an impressive maximum, but autumnal and winter samplings indicated that its offspring, confronted by a large population of predatory *Palpomyia,* and a large fish population in early winter, followed by an extended anaerobic period, did not survive. The winter population of *Chaoborus,* although only about $1/5$ as great as the year before, was somewhat more impressive.

These rather extensive data suggest that sweeping conclusions as to the quantitative interaction of food groups under natural conditions should be made with caution. At the beginning of these surveys it was optimistically expected that the food groups would show seasonal periodicity somewhat comparable from one year to the next, and that although species-substitution might occur

within a food group, the "balance of nature" would rapidly re-establish an equilibrium between the food groups. Such is certainly not the case, at least in the senescent lake. While the relationships of nannoplankton to rotifers, and those of net plankton to *Chaoborus*, have been noted as suggesting predator-prey dynamics, gross productivity (utilization of dissolved nutrients), browsers and predators varied tremendously and independently.

The well-known annual variations in terrestrial communities are usually ascribed to climatic changes. Marked variations in the benthic invertebrates of coastal waters are believed to be partly due to physical conditions during the transition from the pelagic to the benthic stage in the life histories of the organisms (Blegvad, 1925). Eight-fold variations in the numbers of *Chironomus* larvae in a large eutrophic lake (Grosser Plöner See) between 1923 and 1925 were reported by Lundbeck (1926), for which he advanced no explanation. On the other hand, the exended studies of Lake Mendota, Wisconsin, covering a period of many years (Juday, 1940), failed to show such variations.

The annual variations in Cedar Bog Lake can be partly attributable to such indirect climatic effects as water level, duration of winter anaerobiosis, water temperature, climatic conditions during the mating season (for aquatic insects), drainage, etc. Certain unknown trophic relationships, such as growth rate in relation to temperature, disease and parasitism, may also be involved, but it is believed unlikely that browser populations were in any way limited by lack of food. For the predators, of course, such a generalization cannot be made.

In summary, the above quantitative analysis of seasonal food-cycle dynamics over a four-year period suggest the following conclusions: (1) an abundance of green plants as producers does not necessarily indicate an abundance of animals as consumers; (2) remarkable annual variations occur in all food groups of a natural population; (3) apparent predator-prey relationships often prevail between *Chaoborus* larvae and net plankters; and (4) climatic factors, resulting in water level changes, winter anaerobiosis, etc., play an important role in the annual productivity of Cedar Bog Lake.

Biological Productivity

Productivity is a rather loosely used term which indicates the general rate of production of any or every food group in a lake; depending upon how much of the food cycle is to be emphasized, one may speak of gross (or biological) productivity, plankton productivity, zooplankton productivity, bottom-fauna productivity, fish productivity, etc. The amount of substance produced per year, an arbitrary time unit, is known as the annual production, and is a convenient basis for expressing productivity. The quantity usually measured in routine surveys is biomass or "standing crop," a quantity which at best only partially reflects the productivity. The rates of production and consumption of food continually change throughout the year; diversified aquatic producers, including pondweeds, phytoplankton algae and autotrophic

bacteria, possess differential rates of growth, reproduction and completion of life cycle. Juday (1940) estimates that "the average turnover in the organic matter of the mean standing crop of plankton takes place about every two weeks throughout the year." The pondweeds usually develop but one generation per year, while the bacteria may divide several times per day. The year is generally the most useful time unit for expressing productivity.

The production per year includes only a single crop of pondweeds and pondweed epiphytes, but many "crops" of phytoplankters, which have been synthesized, partly consumed, decomposed and resynthesized several times from parts of the same original supply of essential nutrients. In stratified lakes dying phytoplankters during the summer months settle largely undecomposed into the hypolimnion, where a considerable portion of the released nutrients are not again available for synthesis until the fall overturn; these redissolved nutrients are then available, of course, for the large autumnal and vernal pulses of nannoplankton. Thus it is hardly fair to compare the total annual production of phytoplankton with the annual production of pondweeds. Recognition of this inherent error in the given method for evaluating total annual production of a lake is essential for the comparison of productivity between lakes.

The processes responsible for the productivity of any food group are extremely complex and very incompletely understood. Determinations of quantitative values for the annual production of certain groups are fraught with many uncertainties and arbitrary assumptions. In the present inadequate status of our knowledge, it may be argued by some that quantitative estimates of food-group productivity are futile until more definite information has been acquired. In response to which, the author can only plead that for the purpose of tentatively testing certain widely accepted "principles" based largely on theory and qualitative observations, rough approximations of quantitative trophic values are better than none.

The gross production of Cedar Bog Lake can be expressed in terms of the total annual production of pondweeds and of phytoplankton. The maximum or mature standing crop of pondweeds (including pondweed epiphytes) is taken as equivalent to the annual production. The phytoplankton is rather arbitrarily considered to complete a life cycle every week during the summer months (May-September) and every two weeks during the remainder of the year (cf. Juday, 1940). The annual phytoplankton production thus represents the sum of the weekly and biweekly "standing crops" indicated in Fig. 5 (p. 662). The zooplankton is arbitrarily considered to complete a life cycle every two weeks throughout the year. The plankton predators (*Chaoborus* larvae) are believed to develop three generations per year, while both the browsers (chiefly midge larvae) and the benthic predators (chiefly *Palpomyia* larvae) are believed to average about two generations per year in this lake (Lindeman, 1942b). The swimming predators are assumed to develop an average of one generation per year. The annual production of each of these food groups, calculated in approximately the same manner as Juday's (1940) data, is presented in Table 4.

TABLE 4.—Annual Production of Food Groups in Cedar Bog Lake, as cal/cm².

	1937	*1938*	*1939*	*1940*	*Mean*	*S.E.*
Nannoplankters	19.6	20.4	16.7	9.9	16.7 ±	2.2
Net phytoplankters	1.5	9.8	18.9	6.3	9.1 ±	3.7
Pondweeds	63.0	10.5	35.0	70.0	44.6 ±	9.7
Zooplankters	8.5	5.3	7.4	3.2	6.1 ±	1.2
Plankton Predators	0.1	0.3	1.9	0.9	0.8 ±	0.4
Browsers	1.0	0.3	1.0	1.0	0.8 ±	0.2
Benthic Predators	0.1	0.2	0.1	0.4	0.2 ±	0.07
Swimming Predators	0.5	0.1	0.4	0.4	0.3 ±	0.13
Total Producers	84.1	40.7	70.6	85.9	70.3 ±	10.14
Primary Consumers	9.5	5.6	8.4	4.2	7.0 ±	1.07
Secondary Consumers	0.7	0.6	2.4	1.7	1.3 ±	0.43
Total Consumers	10.2	6.2	10.8	5.9	8.3 ±	1.22

The extreme annual variation observed in the seasonal food-group diagram (Fig. 5, p. 662) is also very apparent in these annual productivity values. Nannoplankters are the least variable of the food groups, while the plankton predators are the most variable. When the producers, primary consumers and secondary consumers are totaled separately, the annual productivity is more constant. This decrease in variability suggests a certain amount of "compensation," or transfer of function from one food group to another, within these larger categories.

The efficiency of food conversion from one consumer group to another may be evaluated by comparing the amount of food ingested with the resultant amount of growth. This experimental method, which has been applied to very few organisms, gives conversion factors varying according to stage of development, environmental conditions, etc. The growth efficiency of fishes under laboratory conditions is reported as 43.5% (Moore, 1941), 30% (Detwiler, 1930) and 13% (Dawes, 1931). Under field conditions the reported efficiency ratios of fishes, as would be expected, are much lower: 6% (Bajkov, 1932) and 5.5% (Peterson, 1918). Lundbeck (1926) calculated a rough conversion ratio of 13-14% for *Chironomus* larvae. Juday (1940) has used 20% as an arbitrary physiological efficiency ratio for all animals. The theoretical aspects of apparent and true food-group efficiencies for Cedar Bog Lake will be discussed in detail in a forthcoming paper.

The relative productivities of food groups under natural conditions reflect the physiological efficiency ratios only when food is the sole limiting factor in natural populations. Since food is seldom the only limiting factor, the production-ratios between food groups under natural conditions provide at best only crude indices of actual efficiency. As was previously mentioned, food groups are rather arbitrarily delimited: all the organisms of one group need not be completely dependent upon the food group with which that group is compared; a certain excess of food must always remain unconsumed, in conformity with the principle of Le Chatelier; furthermore, in such a broad unit as predators, for example, may exist many internal predator-prey relationships. Efficiency ratios based on natural populations should not, therefore, be taken too literally. Table 5, which gives various food group ratios for Cedar Bog

TABLE 5.—Percentage Ratios of Food Groups in Cedar Bog Lake, calculated from data of Table 4.

	1937	*1938*	*1939*	*1940*	*Mean**
Zooplankters/Nannoplankters	43.4	25.6	43.4	32.3	37.0
Plankton Predators/Zooplankters	1.2	5.5	25.6	28.8	13.4
Plankton Predators/Net Plankters	1.0	2.0	7.2	9.4	5.6
Benthic Predators/Browsers	10.0	67.6	10.0	40.0	25.0
Browsers/Producers	1.2	7.4	1.4	1.2	1.1
Benthic Predators/Producers	0.1	0.5	0.1	0.6	0.3
Swimming Predators/Producers	0.7	0.3	0.6	0.6	0.5
Primary Consumers/Producers	11.3	13.8	11.9	4.9	9.6
Secondary Consumers/Producers	0.8	1.1	3.4	2.0	1.8
Secondary Consumers/Primary Consumers	6.7	10.8	28.6	40.0	18.5

* The figures in this column represent the ratios between the mean values given in Table 4, rather than the means of the ratios shown in this table.

Lake, shows such extreme annual variation that the mean ratios must be interpreted with considerable regard for their deviations.

The very high ratio between nannoplankters and zooplankters is understandable in view of the ability of zooplankters to feed upon floating organic particles as well as nannoplankters. The ratio of *Chaoborus* larvae (plankton predators) to net plankters appears to remain low; re-examination of Fig. 5 p. 662), however, indicates that during certain seasons the ratio is much higher. The ratio between benthic predators and browsers for 1938 and 1940 appears to indicate a sub-minimal food supply for the former; it is quite probable that food-substitution (browsing?) may have considerably alleviated such a condition.

The relation between consumer and producer groups is very interesting. Both browsers and zooplankters are here considered as primary consumers, neglecting for the sake of simplicity the intermediate action of bacteria on those foods consumed as ooze. During three of the four years studied, the annual ratio of primary consumers to producers was 11.3-13.8%, values remarkably similar to that given by Lundbeck (1926) for the theoretical efficiency of *Chironomus* larvae. The major component of this primary consumer group, however, consists of zooplankters which at least after death may be consumed by the ooze browsers. The considerably lower ratio of browsers to producers (1.1%) gives an indication of the relative efficiency of "saprophagy" in Cedar Bog Lake.

The ratio of secondary to primary consumers gives a mean value of 18.5%, approximately the value (20%) assumed for the physiological efficiency of all animals by Juday. It will be observed that during 1939 and 1940, the ratio was well above this mean; during these years, however, the predator population consisted to a large degree of *Chaoborus* larvae, which, as we have already mentioned, appear to have been at least partly herbivorous. The well known ability of predators to vary their food habits under force of circumstance makes most hazardous the determination of "starvation thresholds" from

natural productivity data. Such data do have value, however, both in indicating the variations found between related food groups and in broadly defining the dimensions of the Eltonian Pyramid for the particular community concerned.

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Summary

1. Cedar Bog Lake, which has been the subject of a four-year study in dynamic ecology, represents a late stage of eutrophic senescence.

2. A generalized diagram of food-cycle relationships is presented: the autotrophic plants, free-floating and attached, are the producers of organic substance; numerous animal groups play intricate, inter-related roles as primary, secondary, tertiary, etc., consumers of this organic substance; heterotrophic bacteria act as decomposers of organic substance and, from another point of view, as regenerators of essential plant nutrients, which again contribute to the synthesis of organic substance.

3. The biotic inter-relationships of the various consumer groups, particularly the browsers, benthic predators and swimming predators, are discussed in some detail.

4. The quantitative seasonal distribution of food groups showed remarkable variation from year to year. These annual variations seemed to be correlated at least in part with marked fluctuations in water level and in chemical composition of the water. Prolonged winter anaerobiosis often completely destroyed the swimming predators and decimated the numbers in other food groups.

5. Climatic variations, resulting in water level changes, winter anaerobiosis, etc., played an important role in the annual productivity of this senescent lake.

6. Limited predator-prey dynamics were suggested in the population ratio of zooplankters to nannoplankters and of *Chaoborus* larvae to net plankters

(Fig. 5). Plankton predators were relatively the most variable of the food groups with respect to annual production, while nannoplankters were relatively the least variable.

7. The mean annual ratios of producers to primary consumers to secondary consumers (including the small swimming predators found in the lake) were: 70.3:7.0:1.3 cal/cm^2. Annual variation was relatively greatest for the secondary consumers and least for the producers.

8. The relative annual production of the food groups, as might be anticipated on theoretical grounds, indicates an efficiency of food conversion much lower than the probable physiological efficiency ratios of the species. Only occasionally did the factor of food supply appear to limit the production of a food group.

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Studies in Ohio Floristics. I.*

Vegetation of Ohio Bogs

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Introduction

The word "bog" has almost as great a variety of meanings as the phrase "typical bog plants." To one person it means a quiet, woodland pool; to another it means a poorly drained depression in a highway, while to a third it creates a mental picture of bleak, Scottish moors. This wide range of interpretation has led to a great deal of confusion when botanists use the term "bog plants."

It is therefore necessary to define the word "bog" as it is used in this study. In so doing it will be necessary to try to separate it from the closely associated words "swamp" and "marsh." It must be borne in mind, however, that on a given terrain any one of these physical conditions may, and usually does, intergrade into one or both of the others. Any one of them may, and frequently does, develop into one of the others, as has been frequently observed and recorded by students of physiography and vegetational history of various regions.

The soils of bog areas are for the most part composed of organic materials in different stages of decomposition. Since these soils are relatively free from colloidal inorganic materials, they remain quite porous and have a "spongy feel" when walked upon or compressed between the hands. The water content of these soils is usually high, but in seasons of low rainfall or following drainage it may become low enough to allow the surface layers of partly decomposed organic materials to burn readily when ignited. The vegetation cover of bogs may show great variations in composition, resulting from the combined effects of numerous factors which will be discussed later. The dominant associations of functional bogs, however, consist of plants whose distribution is confined for the most part to areas composed of soils having the characteristics mentined above. The term "functional bogs," as used in this study refers to bog areas which are not occupied by closed associations of the climatic climax of the region.

A marsh differs from a bog in that the soil contains a higher percentage of inorganic material and is consequently more compact. A marsh may become quite dry in early autumn or during seasons of drought, but it is free from the incendiary possibilities of many bogs because of the lower content of organic materials. The vegetation cover of marsh lands usually consists of associations of grass-like plants.

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Compared with the soils of marshes, swamp soils contain a still higher percentage of inorganic materials. They are free from submergence for longer periods and are consequently better aerated than the soils of either the marshes or bogs. Like the bog, a swamp may be covered with mixed associations of trees, shrubs, and herbs. The dominant species comprising these associations, however, are strikingly different from those of the immature bog.

Location and Extent of Ohio Bogs

Accurate information pertaining to the exact location and extent of Ohio bogs as they are considered in this study is not available. A slightly revised and modified reproduction of Dachnowski's peat deposit map (2), however, will give a general idea of the location of the major bog areas in the state at the time of settlement. As one might suspect, the actual area occupied by functional bogs, as dealt with in this study, is much smaller than the map

Fig. 1. Bog areas in Ohio at time of white man's occupation.

would lead one to believe. The 155,047 acres of peat land, as estimated for Ohio by the federal government, has been greately exaggerated on this map, and when we consider the number of acres which have been cleared, burned, and drained we begin to see what a very small area functional bogs really occupy in the state. In many instances the presence of dark colored soils is the only indication of the bog vegetation which once occupied the area.

Conditions Necessary for Bog Formation

When we recall the great variety of habitats on which bogs may occur in widely separated regions of the earth, we are inclined to think that the conditions under which bogs are formed must not be very exacting. Such, however, is far from the truth. When we consider the ecological environments of bogs in Siberia, central United States, and some countries in South America we find that they have many factors in common. Some of the conditions necessary for bog formation and continuation are as follows:

1. The water supply must be constant enough to prevent the establishment of dry land associations. This condition may occur in depressions, either deep or shallow, where outlets are poorly developed or internal drainage is poor. In the plateau section of the state this condition may be maintained by the flow of spring water over terraces or hill sides.

2. The area must be relatively free from deposition of inorganic materials. The deposition of inorganic materials soon converts bogs into marshes and swamps.

3. Growing seasons must be sufficiently long to permit the production of a vegetation cover.

4. Conditions must be such that plant materials are not oxidized too rapidly or too completely by the action of bacteria and fungi.

5. Light conditions must be optimum during the growing season. Many woodland pools would soon be converted into bogs if there were sufficient light for luxuriant plant growth.

Classification of Bogs

Ohio bogs may be classified in a great many ways. The most important, perhaps, are the following:

A. Physiography.

B. Method of development.

C. Vegetation cover.

A. According to their physiography bogs may be divided into bogs formed *in* basins or depressions and those formed *on* flat or sloping surfaces.

I. Basin or depression bogs may be subdivided in those formed in:

1. Kettle-holes.
2. Depressions between sand dunes.
3. Depressions behind dams which have been formed by:
   a. Glacial deposits.
   b. Wind, wave, and ice action along lakes.
   c. Streams cutting off ox-bows and deposition occurring at the "points" of the bow.
   d. Slumps, landslides, talus, driftwood, and deltaic deposits.

II. Level or sloping surface bogs may be subdivided into those formed on:

1. Poorly drained till plains.
2. Broad divides.
3. Glacial valley floors.
4. Terraces.
5. Deltas.
6. Slopes over which spring water flows.

B. According to the method of their development bogs may be divided into:

I. Bogs formed in shallow depressions or on flat surfaces by successive generations of plants growing upon the remains of the previous year's vegetation cover. This type of growth occasionally results in the "raised" type of bog.

II. Bogs formed in lakes, ponds, or sluggish streams from deposits of plant mats which have been growing on the surface and sides of the depression. Plants floated into the area from an outside source may also contribute to these deposits.

C. According to their vegetation cover bogs may be separated into an almost endless number of divisions. Some of the factors influencing these variations are as follows:

I. Age of the bog.

II. Constancy of the water supply.

III. Maximum and minimum air, water, and soil temperatures. This factor may be greatly influenced by the existing vegetation cover and the geographical location.

IV. Mineral content of the water.

V. Source of vegetation cover.

VI. Light. The existing vegetation cover may have a very marked influence on the intensity and duration of the light reaching the lower strata of vegetation.

Genetic Development

When we consider the genetic development of Ohio bogs in relation to the development of a vegetation cover we are at once confronted with a great many complex problems, because of the fact that the developmental history of a bog area is seldom a clear-cut series of events from an open water or bare soil area to one covered by climax vegetation. Two bog areas, located relatively near to each other, seldom have the same genetic history. This is well illustrated by the raised bog at Urbana, the bog at Cedar Swamp, and the lake margin bog at Brush Lake, all located within a few miles of each other in Champaign County.

Some of the problems which must be considered when investigating the genetic history of the vegetation cover of a bog area are as follows:

1. Raising or lowering of the water level due to local disturbances. Such occurrences may result in the retarding, speeding up, or complete elimination of some stages of vegetation development. Davis, in his work on the peat deposits of Michigan (3), reports numerous instances in which the vegetation cover of spruce- and tamarack-covered bogs has been destroyed following the construction of dams by beavers. In one instance three such dams were encountered during the construction of a drainage ditch, the first 4 feet under the peat, the second 10 feet, and the third 12 feet.

2. Deposition of inorganic sediments. When drainage changes, such as the shift of a stream from one side of a valley to the other occur, deposition of inorganic sediments may rapidly convert bog areas into marshes or swamps with their characteristic vegetation cover. Schaffner and others have observed this phenomenon in relation to cultivated fields surrounding Brush Lake (7).

3. Type of land surface and method of development. It is quite obvious that the vegetation history of a bog developed on a slope below a spring and one developed in a deep water basin would be quite different. On flat or sloping land surfaces the environmental conditions may be such that almost any stage in the usual genetic development of bog vegetation as found in basins may come into being in a relatively short period of time.

4. Climatic changes and sources of vegetation. The dominant vegetation cover of many bog areas in northern Ohio is undoubtedly of boreal origin and represents relics of former climatic conditions. For example, in northeastern Ohio bogs one finds *Larix laricina, Pinus strobus,* and *Betula lutea;* while in southern Ohio *Platanus occidentalis, Celtis occidentalis,* and *Populus deltoides* are the dominant trees in many bogs. Extensive bog areas located on flat surfaces and in shallow depressions must have been converted into "wet prairies" following the advance of prairie vegetation into the state during the post-glacial Xeric Period (8).

5. Effects of man's occupation. In almost all of the bog areas in the state today the natural process of bog vegetation succession has been altered by man's activities. Historians tell us that the firing of bog areas in autumn in order to drive out the game was a common practice of both the Indians and

white settlers (2). Vast areas have been drained, cleared, and converted into ponds and lakes by the construction of artificial dams. The presence of numerous introduced European weeds in all relatively undisturbed Ohio bogs indicate the indirect effect which man may have on the vegetation cover of such areas.

Bog vegetation on relatively flat terrain is seldom distributed in zones. Slight depressions and elevations result in a complex pattern of mature and

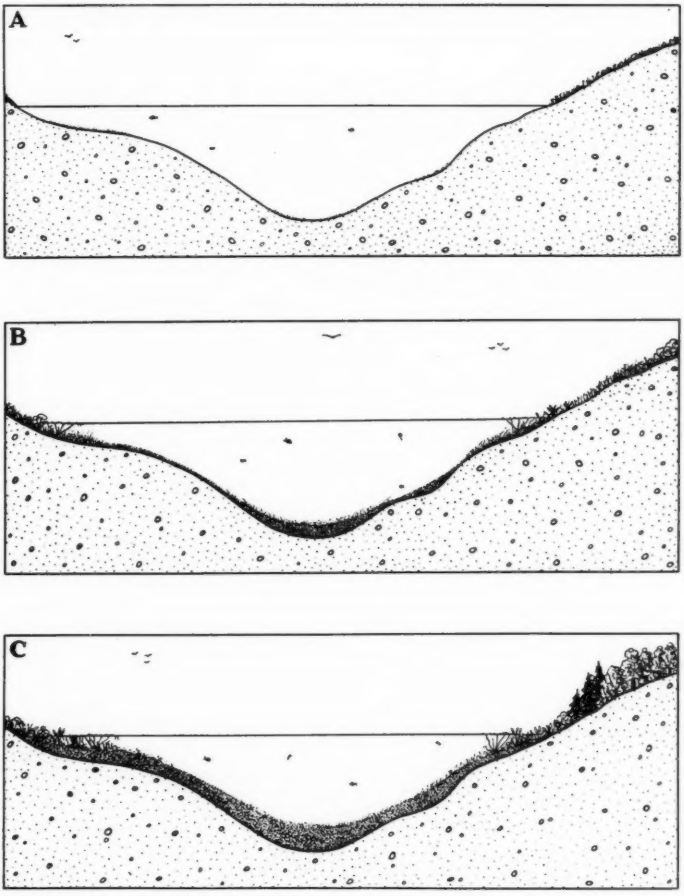

Fig. 2. Stages in the development of bog vegetation in a lake basin.

juvenile bog species. The vegetation cover of bog areas located in basins, however, is usually distributed in more or less well defined zones, and from these zones one can gain a rather definite concept of the stages of vegetation development.

We do not have any accurate method of determining the composition of the first plant associations to inhabit open water areas following the retreat of the various ice sheets which have invaded Ohio in prehistorical times. We can, however, after investigating the vegetation cover of numerous bogs in different stages of development and observing the invasion of plants into newly created water bodies, gain some idea of the various developmental steps.

Stage I

The first stage in plant occupation of open water bodies is the development of plankton associations consisting of bacteria, desmids, diatoms, and many kinds of single- and multiple-celled algae. Most of these ancient and relatively simple forms of plant life are confined to the surface of the water, but in some instances filamentous algae may occur as much as 30 feet below the surface. These plankton associations consist of both autophytic and saprophytic forms; and, while the organisms themselves add but little to the organic content of the soil, they play a very important part in its formation (Fig. 2A).

Stage II

In a zone extending from the shore line to a depth of 15 or 20 feet, associations of attached aquatics, free-floating aquatics and semi-aquatics begin to appear (Fig. 2B). Some of the representative species of this zone are as follows:

Castalia odorata
Ceratophyllum demersum
Chara foetida
Elodea canadensis
Lemna minor
Myriophyllum spicatum
Najas flexilis
Nelumbo lutea
Nymphaea advena
Peltandra virginica
Polygonum amphibium
Pontederia cordata
Potamogeton pectinatus
Proserpinaca palustris
Riccia fluitans
Ricciocarpus natans
Spirodela polyrhiza
Utricularia vulgaris
Wolffia columbiana
Zannichellia palustris

If the water in which the aquatic associations are growing is of relatively uniform depth there is but little tendency toward zonation within the group. In many instances, however, the water becomes deeper toward the center of the basin. When this condition exists definite zonation is usually evident, with *Chara, Elodea, Myriophyllum, Ceratophyllum, Utricularia,* and *Potamogeton* occupying the deeper water, and *Nelumbo, Pontederia, Nymphaea, Castalia, Polygonum,* and *Peltandra* the shallow. The free-floating aquatics are distributed indiscriminately among the members of the second group.

Stage III

Following, or contemporary with, the second stage, a zone of terrestrial and semi-aquatic plants appears in and at the water's edge. These plants are

the true forerunners of the typical bog vegetation and are frequently called the shoreline associations. There are no sharp lines of demarcation between the various associations of this zone and the zone preceding or following it (Fig. 2C). This zone, is "characterized by plants which have their roots, rhizomes, and the lower parts of their erect stems exposed to aquatic conditions" (7). Some of the important species comprising the associations of this zone are the following:

Alisma plantago-aquatica
Bidens cernua
Carex aquatilis
Cephalanthus occidentalis
Cicuta bulbifera
Cyperus strigosus
Decodon verticillatus
Glyceria nervata
Juncus brachycephalus
Leersia virginica
Polygonum amphibium
Radicula palustris
Ranunculus pennsylvanicus
Rumex britannica
Sagittaria latifolia
Salix nigra
Scirpus validus
Solanum dulcamara
Sparganium eurycarpum
Typha angustifolia

Stage IV

When plants of the shoreline associations increase in number and form closed associations, competition for light becomes intense between the individual plants. A gradual invasion of the open water areas and extermination of submerged aquatics at the zone of contact by shading soon follows. This invasion of open water areas is made possible because: (1) Plants of the aquatic and semi-aquatic associations of Stage II have been gradually building up the substratum by the addition of organic material, thereby reducing the depth of the water and bringing into being conditions which favor the establishment of the semi-aquatic and terrestrial plants of Stage III. (2) Some species have the ability to form floating, mat-like extensions of living plants on the surface of the water. This mat formation also results in extermination of the attached aquatics of Stage II by reducing the amount of light which reaches them. Some of the species which have this mat forming ability are *Carex filiformis, C. limosa, C. oligosperma, C. rostrata, Solanum dulcamara, Cephalanthus occidentalis, Chamaedaphne calyculata,* and *Decodon verticillatus.*

As this shoreline zone of vegetation advances into the open water areas it creates conditions unfavorable for its own perpetuation and continuation in the area between it and the edge of the unsubmerged terrain where it originated. This condition comes into being when: (1) The floating mat becomes established sufficiently to reduce the light enough to prevent the re-establishment of annuals and growth of perennials of the semi-aquatic members of the association. (2) The constant addition of organic materials has created conditions favorable to the invasion and establishment of plants better adapted to this newly created habitat.

As soon as the above conditions have become established bog meadow associations invade the area between the shoreline zone and the terrain of its origin (Fig. 3D).

Some of the representative species of this bog meadow zone are as follows:

Arethusa bulbosa
Asclepias incarnata
Aspidium thelypteris
Aster puniceus
Calopogon pulchellus
Caltha palustris
Cardamine pennsylvanica
Carex comosa
Drosera rotundifolia
Dulichium arundinaceum
Eleocharis palustris
Epilobium adenocaulon
Eriophorum virginicum
Galium boreale
Gentiana crinita
Glyceria canadensis
Juncus effusus
Lobelia cardinalis
Menyanthes trifoliata
Osmunda cinnamomea
Panicum implicatum

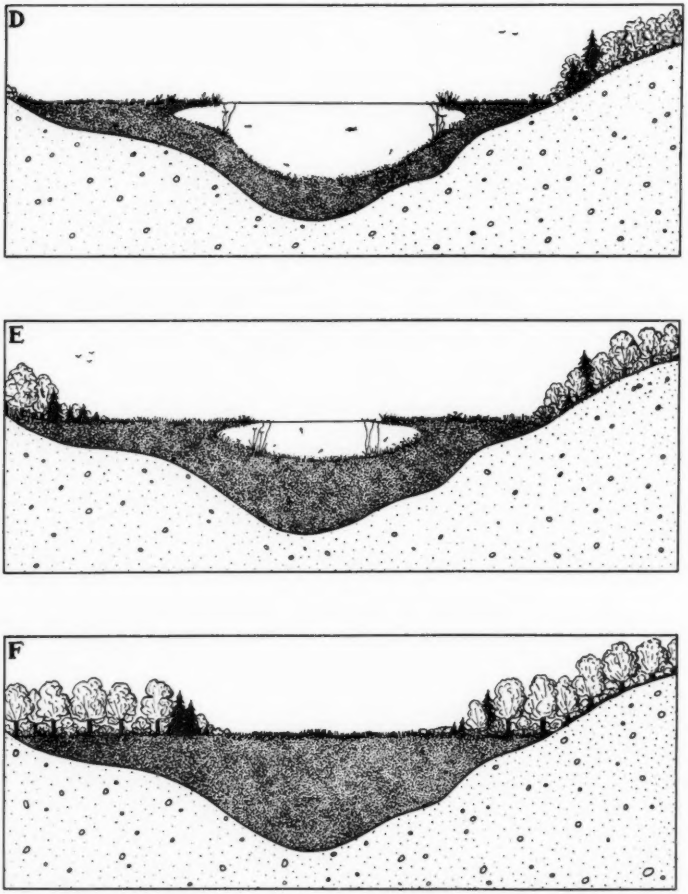

Fig. 3. Stages in the development of bog vegetation in a lake basin.

Parnassia caroliniana
Pellandra virginica
Penthorum sedoides
Pogonia ophioglossoides
Potentilla palustris
Rubus triflorus
Rynchospora glomerata
Sagittaria latifolia
Sarracenia purpurea
Scheuchzeria palustris
Scirpus cyperinus
Solidago rugosa
Sparganium eurycarpum
Spartina michauxiana
Typha latifolia
Urtica gracilis
Vaccinium macrocarpon
Verbena hastata
Xyris flexuosa

North of Ohio, members of the heath family frequently form dominant associations in the bog meadow zone. In Ohio, however, this is seldom the case. In Portage and Ashtabula counties some bog meadows are dominated by *Chamaedaphne calyculata, Andromeda polifolia, Vaccinium* sp., *Gaylussacia baccata* and *Gaultheria procumbens* associations. *Gaylussacia baccata* and *Vaccinium* sp. are important members of the bog meadow associations of Cranberry Island in Licking County, and *Potentilla fruticosa* is of equal importance in the Cedar Swamp bog in Champaign County and the Big Spring Prairie bog in Wyandot County. Historical records indicate that many other northern Ohio bogs had heath associations at the time of settlement.

In numerous bog areas, especially in the southern half of the state, Stage III is followed by Stage V, the bog shrub zone, instead of Stage IV, the bog meadow zone.

Stage V

Following, or contemporary with, the migration of the aquatic, shoreline, and bog meadow zones toward the center of the basin, a bog shrub association appears at the terrestrial margin or oldest part of the bog meadow zone. The establishment of this bog shrub zone is made possible through the subsequent accumulation, partial decay, and compacting of plant materials of the bog meadow zone, resulting in ecological changes which create environments favorable to the invasion and establishment of bog shrub association (Fig. 3E).

Some of the representative species of this zone are as follows:

Alnus incana
Amelanchier canadensis
Apios tuberosa
Asclepias incarnata
Aspidium angustifolium
Benzoin aestivale
Betula lutea
Bidens coronata
Boehmeria cylindrica
Campanula americana
Celastrus scandens
Cephalanthus occidentalis
Convolvulus sepium
Cornus amomum
Cuscuta grovonii
Rynchospora glomerata
Hypericum punctatum
Ilex verticillata
Impatiens biflora
Ipomoea purpurea
Lonicera canadensis
Menispermum canadense
Monarda fistulosa
Nemopanthus mucronata
Onoclea sensibilis
Physocarpus opulifolius
Psedera quinquefolia
Pyrus americana
Rhamnus alnifolia
Rhus vernix
Ribes cynosbati
Rosa carolina
Rubus hispidus
Rudbeckia speciosa
Salix nigra
Sambucus canadensis
Solanum dulcamara
Spiraea salicifolia
Symplocarpus foetidus
Vaccinium corymbosum
Veronica scutellata
Viburnum dentatum
Vitis vulpina
Zanthoxylum americanum

Stage vi

The invasion of the bog shrub zone by trees from the surrounding uplands may occur simultaneously with, or soon after, its establishment. In areas where soil building is proceeding at a slow rate toward the center of the basin the trees may soon over-top the bog shrub associations resulting in an early elimination of the species which are less shade-tolerant. When this condition exists we find the tree zone bordering the bog meadow or the shoreline zone if a bog meadow has not been developed. The soil-building activities of the numerous associations which have migrated toward the center of the basin, however, are usually rapid enough to permit a zone of shrubs to migrate ahead of the invading tree zone (Fig. 3F).

The invasion of the landward edge of the shrub zone by conifers, which is the usual succession in Canadian bogs, is exceptional in Ohio. In Portage, Geauga, Williams, and Ashtabula counties, however, remnants of one type of this conifer invasion are evident. *Larix laricina* is the dominant in this *Larix laricina-Pinus strobus-Tsuga canadensis* association. A second type of conifer invasion is evident in the Cedar Swamp bog in Champaign County, where a *Thuja occidentalis* association exists. Here and there, scattered through the above associations, are occasional specimens of *Taxus canadensis* and *Betula lutea*.

The existence of conifer associations is of little importance from the viewpoint of genetic development of the vegetation cover in the majority of Ohio bogs today, since these associations are but remnants of a post-glacial period when conifer associations were dominant in this region.

The following species list is representative of the deciduous trees which invade the bog shrub zone, or the conifer zone if one is present, in Ohio bogs:

Acer rubrum
Celtis occidentalis
Fraxinus americana
Fraxinus nigra
Gleditsia triacanthos
Juglans cinerea
Juglans nigra
Liriodendron tulipifera
Platanus occidentalis
Populus deltoides
Prunus serotina
Quercus bicolor
Quercus macrocarpa
Quercus palustris
Ulmus americana
Ulmus fulva

The following list of shrubs, vines, and small trees many of which are also found in the bog shrub zone, is representative of the shrub layer beneath the trees:

Alnus incana
Amelanchier canadensis
Asimina triloba
Benzoin aestivale
Betula lutea
Carpinus caroliniana
Celastrus scandens
Cercis canadensis
Cornus stolonifera
Evonymus atropurpureus
Ilex verticillata
Menispermum canadensis
Morus rubra
Ostrya virginiana
Psedera quinquefolia
Rhamnus alnifolia
Rhus vernix
Prunus serotina
Pyrus americana
Ribes cynosbati
Salix cordata
Sambucus canadensis
Viburnum dentatum
Vitis vulpina

The following species are frequently found in the ground-cover vegetation:

Adiantum pedatum
Arabis laevigata
Aralia racemosa
Arisaema triphyllum
Aster paniculatus
Cardamine bulbosa
Carex lurida
Caulophyllum thalictroides
Claytonia virginica
Clintonia borealis
Coptis trifolia
Cystopteris fragilis
Dalibardia repens
Elymus virginicus
Eupatorium purpureum
Galium asprellum
Geum canadense
Impatiens biflora
Lycopodium lucidulum
Medeola virginiana
Mianthemum canadense
Mitella diphylla
Osmunda cinnamomea
Phlox divaricata
Podophyllum peltatum
Polystichum acrostichoides
Ranunculus recurvatus
Rubus procumbens
Sanguinaria canadensis
Sanicula canadensis
Smilacina racemosa
Solidago canadensis
Thalictrum dioicum
Trientalis americana
Trillium grandiflorum
Urtica gracilis
Veronica serpyllifolia
Viola blanda

We must not lose sight of the fact that as successive zones of vegetation have come into being near the margins of the area, there has been a gradual migration toward the center of the basin by the preceding zones (Fig. 3F). The rate of speed at which this zonal migration occurs depends upon a great many factors, the most important of which is probably the topography of the basin itself. In basins with steep under-water slopes all of the stages or vegetation zones, from the open-water associations near the center of the basin to the tree associations at the margins, may be evident. Shallow basins rarely exhibit more than two or three of these zones at one time.

Attention has been called to the fact that the vegetation cover, in any stage of the bog's development, depends upon a great many different factors and that some of the intermediate stages in the usual developmental history may not even appear. Under ideal conditions, however, there is a systematic establishment and gradual migration of individual zones toward the center of the basin as rapidly as the preceding zone has created an environment favorable to the invasion and establishment of succeeding landward zones. By this method of migration the shoreline associations finally meet and the aquatic associations disappear (Fig. 3F). Scattered specimens of the shoreline associations may remain in this central area of the basin for a long time, but in turn they, too, are crowded out by the invading bog meadow associations (Fig. 4G). From the older and dryer parts of the bog meadow the scattered colonies of bog shrubs gradually migrate into, and finally dominate, the entire area (Fig. 4H). In turn, the bog shrubs are over-topped by invading tree associations of the climax vegetation of the region. Conifer associations, if present, usually migrate into and dominate the central area ahead of the deciduous associations (Fig. 4H). When this condition does occur the conifer associations are soon over-topped and succeeded by the more shade-tolerant species of deciduous trees (Fig. 4I). This invasion of forest trees, followed by composition modifications or complete disappearance of shrub associations, terminates the natural genetic history of the vegetation cover of the area.

Bog Vegetation

A great variation in plant species and associations may be expected among individual bogs, and no attempt has been made to include all of the plants

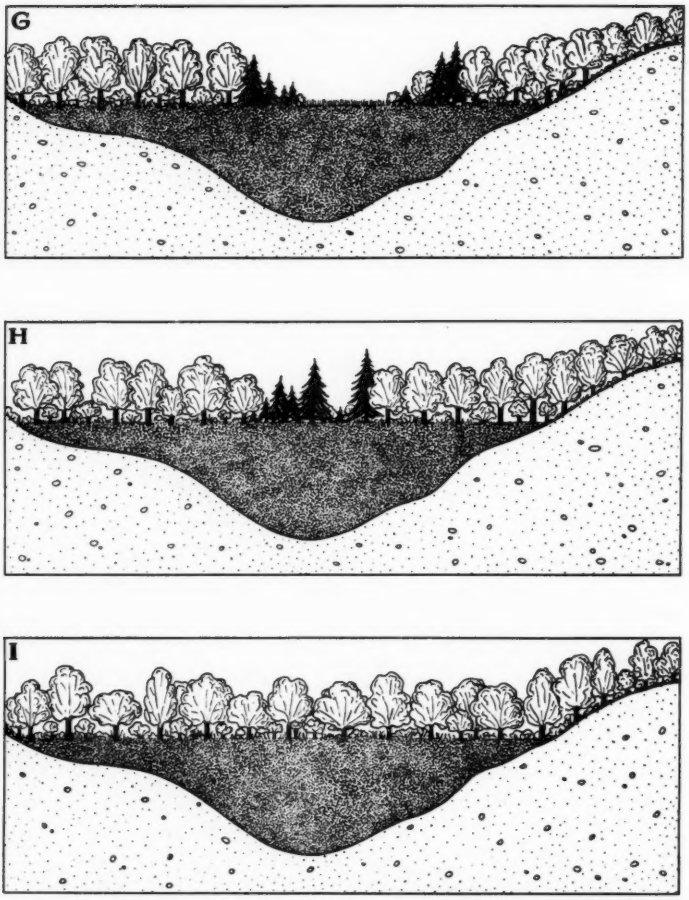

Fig. 4. Stages in the development of bog vegetation in a lake basin.

which may occur in Ohio bogs. The numerous factors influencing these variations have already been mentioned.

Many of the plants which have been listed as typical bog plants could not be so classified a few hundred miles north or south of their Ohio habitat. In central Ontario, for instance, *Linnaea borealis* and *Rubus triflorus* may be frequently found growing on moss-covered boulders high in the uplands, while a few miles south of the Ohio River *Lyonia ligustrina* and *Parnassia*

caroliniana may be found growing in swamps and on wet rocks. Most of the plants which are usually classified as true aquatics by botanists have been purposely excluded, and only terrestrial and semi-aquatic plants which have been collected in Ohio bogs and are now in the State Herbarium have been listed.*

The first section consists of plants which are confined, for the most part, to bog habitats in Ohio and may be classified as typical bog plants.

Alnus incana
Andromeda polifolia
Arethusa bulbosa
Betula pumila
Calla palustris
Calopogon pulchellus
Campanula aparinoides
Carex incomperta Bickn.
Carex filiformis
Carex limosa
Chamaedaphne calyculata
Chiogenes hispidula
Coptis trifolia
Cypripedium candidum
Cypripedium parviflorum
Cypripedium hirsutum
Dalibardia repens
Decodon verticillatus
Drosera rotundifolia
Drosera longifolia
Dulichium arundinaceum
Eriophorum virginicum
Eriophorum viridi-carinatum
Galium labradoricum
Gentiana crinita
Habenaria blephariglottis
Habenaria hyperborea
Ilex verticillata
Larix laricina
Ledum groenlandicum
Liparis loeselii
Lonicera oblongifolia
Lyonia ligustrina
Menyanthes trifoliata
Nemopanthus mucronata
Parnassia caroliniana
Peltandra virginica
Pogonia ophioglossoides
Potentilla fruticosa
Potentilla palustris
Pyrus arbutifolia
Pyrus melanocarpa
Rhamnus alnifolia
Rhus vernix
Rubus triflorus
Salix candida
Salix pedicellaris
Sarracenia purpurea
Scheuchzeria palustris
Smilacina trifolia
Trientalis americana
Vaccinium canadense
Vaccinium corymbosum
Vaccinium oxycoccus

Plants of moist habitats which occur in Ohio bogs but are not restricted to typical bog habitats:

Acer rubrum
Adiantum pedatum
Alisma plantago-aquatica
Alnus rugosa
Anemonella thalictroides
Angelica atropurpurea
Apios tuberosa
Aralia nudicaulis
Aralia racemosa
Arisaema triphyllum
Asclepias incarnata
Aspidium goldianum
Aspidium thelypteris
Asplenium angustifolium
Aster junceus
Aster novae-angliae
Aster paniculatus
Aster puniceus
Aster tradescanti
Bartonia virginica
Benzoin aestivale
Betula alba
Betula lutea
Bidens cernua
Bidens coronata
Bidens discoidea Britt.
Bidens laevis
Boehmeria cylindrica
Calamagrostis canadensis
Calamagrostis cinnoides
Caltha palustris
Cardamine bulbosa
Cardamine pennsylvanica
Carex aquatilis
Carex canescens
Carex comosa
Carex cristata
Carex folliculata
Carex frankii
Carex grisea
Carex hystericina
Carex intumescens
Carex lanuginosa
Carex leptalea
Carex lurida
Carex oligosperma
Carex polygama
Carex rostrata
Carex sartwellii
Carex scirpoides
Carex shortiana
Carex sterilis
Carex stipata
Carex tribuloides
Carex trisperma
Carex vulpinoidea
Carpinus caroliniana
Caulophyllum thalictroides
Celtis occidentalis
Cephalanthus occidentalis
Chelone glabra
Cicuta bulbifera
Cladium mariscoides
Clintonia borealis
Cornus alternifolia
Cornus circinata
Cornus stolonifera
Cypripedium acaule
Cystopteris bulbifera
Deschampsia caespitosa
Dianthera americana
Dodecatheon meadia

* Nomenclature essentially that of Gray's Manual, 7th edition.

Eleocharis obtusa
Eleocharis palustris
Elymus virginicus
Epigaea repens
Epilobium adenocaulon
Epilobium coloratum
Epilobium densum
Epilobium molle
Equisetum fluviatile
Eupatorium perfoliatum
Eupatorium purpureum
Evonymus atropurpureus
Festuca rubra
Fraxinus nigra
Galium asprellum
Galium claytoni
Galium tinctorium
Gaultheria procumbens
Gentiana quinquefolia
Geum rivale
Glyceria canadensis
Glyceria nervata
Glyceria torreyana
Habenaria lacera
Habenaria psycodes
Hibiscus moscheutos
Hierochloe odorata
Hypericum mutilum
Hypericum punctatum
Hypericum virginicum
Impatiens biflora
Iris versicolor
Iris virginica
Juncus brachycephalus
Juncus canadensis
Juncus effusus
Lathyrus myrtifolius Muhl.
Lathyrus palustris
Leersia virginica
Linum striatum
Lobelia cardinalis
Lobelia siphilitica
Lonicera canadensis
Ludvigia alternifolia
Ludvigia palustris
Lycopodium inundatum
Lycopodium lucidulum
Lycopodium obscurum
Lycopus americana
Lysimachia thyrsiflora
Medeola virginiana
Menispermum canadense
Mentha arvensis
Mianthemum canadense
Milium effusum
Mimulus ringens
Mitchella repens
Mitella diphylla
Myrica carolinensis
Nymphaea advena
Onoclea sensibilis
Osmunda cinnamomea
Osmunda claytoniana
Osmunda regalis
Ostrya virginiana
Penthorum sedoides
Phragmites communis
Pinus strobus
Platanus occidentalis
Polygonum amphibium
Polygonum hydropiperoides
Polygonum persicaria
Polygonum sagittatum
Polymnia canadensis
Proserpinaca palustris
Pyrus americana
Quercus bicolor
Quercus palustris
Radicula aquatica
Radicula palustris
Ranunculus pennsylvanicus
Rosa carolina
Rubus hispidus
Rumex altissimus
Rumex britannica
Rynchospora glomerata
Sagittaria latifolia
Salix cordata
Salix discolor
Salix lucida
Salix nigra
Salix petiolaris
Salix sericea
Sanguinaria canadensis
Saururus cernuus
Scirpus americana
Scirpus atrovirens
Scirpus cyperinus
Scirpus fluviatilis
Scirpus lineatus
Scirpus validus
Scutellaria galericulata
Scutellaria lateriflora
Senecio aureus
Seymeria macrophylla
Sium cicutaefolium
Solidago neglecta
Solidago ohioensis
Solidago riddellii
Solidago rugosa
Sparganium eurycarpum
Spartina michauxiana
Spiraea salicifolia
Spiraea tomentosa
Spiranthes romanzoffiana
Symplocarpus foetidus
Taxus canadensis
Thalictrum dasycarpum
Thalictrum dioicum
Thaspium barbinode
Thuja occidentalis
Tofeldia glutinosa
Triglochin palustris
Trillium erectum
Trillium grandiflorum
Trillium undulatum
Tsuga canadensis
Typha angustifolia
Typha latifolia
Urtica gracilis
Utricularia cornuta
Utricularia intermedia
Valerianella radiata
Verbena hastata
Veronica arvensis
Veronica peregrina
Veronica scutellata
Veronica serpyllifolia
Viburnum cassinoides
Viburnum dentatum
Viburnum lentago
Viburnum opulus
Viola blanda
Viola lanceolata
Woodwardia virginica
Xyris flexuosa

Plants of wide habitat range which occasionally occur in Ohio bogs:

Ambrosia trifida
Asimina triloba
Arabis hirsuta
Arabis laevigata
Aspidium noveboracense
Aspidium spinulosum
Barbarea vulgaris
Blephillia hirsuta
Camelina sativa
Campanula americana
Carex albolutescens
Carex granularis
Carex scoparia
Carex trichocarpa aristata
Carex tuckermanii
Carex virescens
Carya cordiformis
Cassia marilandica
Celastrus scandens
Celtis occidentalis
Cercis canadensis
Cirsium discolor
Cirsium muticum
Claytonia virginica

Convolvus sepium
Cornus amomum
Cuscuta grovonii
Cyperus strigosus
Cystopteris fragilis
Echinochloa crusgalli
Elymus striatus
Elymus canadensis
Equisetum arvense
Erigeron annuus
Erigeron philadelphicus
Euphorbia corollata
Fraxinus americana
Galium trifidum
Galium triflorum
Gaylussacia baccata
Gerardia paupercula
Geum canadense
Geum virginianum
Gleditsia triacanthos
Habenaria clavellata
Heliopsis scabra
Hypericum prolificum
Hypericum virginicum
Ipomoea purpurea
Juglans cinerea
Juglans nigra
Juncus acuminatus
Juncus tenuis
Lactuca canadensis
Liriodendron tulipifera
Lobelia spicata
Monarda fistulosa
Morus rubra
Nepeta hederacea
Oenothera biennis
Osmorhiza claytoni
Ostrya virginiana
Oxalis grandis
Oxalis violaceae
Panicum capillare
Panicum huachucae
Panicum implicatum
Panicum sphaerocarpon
Pedicularis lanceolata
Phlox divaricata
Physocarpus opulifolius
Phytolacca decandra
Plantago lanceolata
Plantago major
Polygonum muhlenbergii
Polygonum pennsylvanicum
Polystichum acrostichoides
Populus deltoides
Populus tremuloides
Psedera quinquefolia
Podophyllum peltatum
Potentilla monspeliensis
Potentilla canadensis
Prunella vulgaris
Prunus serotina
Pteris aquilina
Quercus imbricaria
Ranunculus abortivus
Ranunculus recurvatus
Ribes cynosbati
Rubus procumbens
Rudbeckia speciosa
Rudbeckia triloba
Rumex acetosella
Rumex crispus
Rumex obtusifolius
Sambucus canadensis
Sanicula canadensis
Sanicula gregaria
Sanicula trifoliata
Scrophularia marylandica
Solanum carolinense
Solanum dulcamara
Solidago canadensis
Taraxacum officinale
Thalictrum dasycarpum
Ulmus americana
Ulmus fulva
Vaccinium pennsylvanicum
Verbascum thapsus
Verbena urticaefolia
Veronica altissima
Veronica officinalis
Viola papilionaceae
Viola pubescens
Zanthoxylum americanum

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Notes on North American Plants — I.

F. R. Fosberg

To take care of such observations on the taxonomy, nomenclature, and distribution of American plants as accumulate in the course of herbarium and field work, it seems worth while to start a series of short papers of a miscellaneous character, dealing with the vascular plants of North America.

Notes are presented in this paper on the genera *Eragrostis (Gramineae)*, *Chenopodium*, *Atriplex (Chenopodiaceae)*, *Oxystylis (Capparidaceae)*, *Rhus (Anacardiaceae)*, and *Acer (Aceraceae)*.

Abbreviations for herbaria are as follows: (USNA), Herbarium of the U. S. National Arboretum; (US), U. S. National Herbarium; (UP), Herbarium of the University of Pennsylvania.

Eragrostis diffusa Buckl.

This species is mentioned from California by Hitchcock (Man. Gr. U. S. 152, 1935) only from Southern California. Munz (Man. S. Cal. Bot. 51, 1935) says "Rare, central Calif. to Mexico and Maine." Jepson (Man. Fl. Pl. Calif. 1923) does not mention it at all. In the U. S. National Herbarium are only two sheets from the San Joaquin Valley: Visalia, *Congdon* in 1881; Fresno, 1933, *Springer 528*. At Turlock, Stanislaus Co., the species is abundant in irrigated land, especially along ditches, and has been, at least as far back as 1920, from my personal recollection. Specimens collected in 1928 and 1937 were submitted to J. R. Swallen, who identified them as this species (*F. R. Fosberg S 704* (UP), *14266* (UP); *K. P. Fosberg* in 1937 (UP)).

Chenopodium fremontii Wats., Bot. King. Exp. 287. 1871.

The differences between several of the species of Chenopodium that have been described from the western United States are neither of such magnitude nor of such constancy as to be very convincing. Such differences between three of what seem to me to be varieties of *C. fremontii* as are sufficient to separate them in most cases are given in the following key.

1. Leaves deltoid, usually noticeably hastate.
   2. Plants strongly branched at base, in outline rounded, often broader than high, stems somewhat coarse ..... var. *incanum*
   2. Plants with a single erect main stem, usually not, or only slightly branched at base, somewhat branched in upper parts, stems slender..... var. *fremontii*

1. Leaves oblong, not or only weakly hastate, usually slender, with obvious erect main stem ..... var. *atrovirens*

Chenopodium fremontii Wats. var. **fremontii,** new name

Chenopodium fremontii Wats., Bot. King Exp. 287, 1871 (sensu str.)

CHENOPODIUM FREMONTII Wats. var. INCANUM Wats., Proc. Am. Acad. 9:94, 1874.

Chenopodium incanum (Wats.) Heller, Pl. World **1**:23, 1897.

Chenopodium fremontii Wats. var. **atrovirens** (Rydb.) n. comb.

Chenopodium atrovirens Rydb., Mem. N. Y. Bot Gard. **1**:131, 1900.
Chenopodium aridum A. Nels., Bull. Torr. Cl. **31**:240, 1904.

The differences between *Ch. atrovirens* and *Ch. fremontii* seem to be very trivial. The leaves of the former are narrower and more acute at base, and the calyx lobes somewhat less carinate. This seems scarcely enough to base species upon, even in *Chenopodium*. Recognition in the varietal category seems sufficient to indicate its slight divergence from the main stock of the species in the direction of *Ch. leptophyllum*. It is quite within the bounds of possibility that there has been extensive hybridization between several native Chenopodiums of the western United States. Careful study of their local distribution might throw valuable light on this matter.

CHENOPODIUM NEVADENSE Standl. N. Am. Fl. **21**:16, 1916.

Chenopodium capillare Jones, Contr. West. Bot. **17**:30, 1930.

In connection with the Indian Drug Plant Project eight collections of this previously almost unknown species were made, providing an opportunity to study it and to establish firmly its validity as a species.

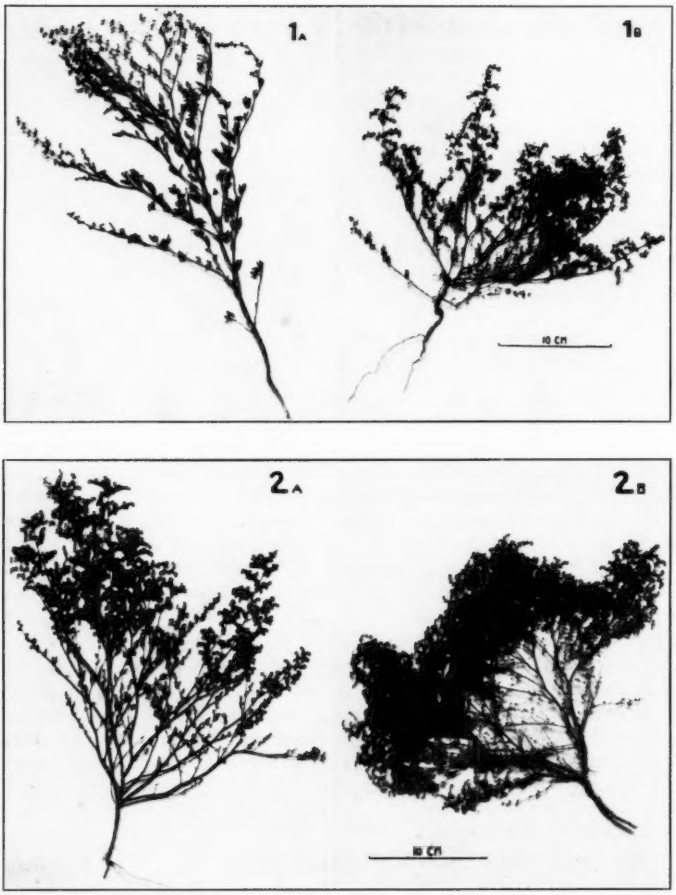
On the type sheet (Winnemucca Lake, Washoe Co., Nevada, *Kennedy 1993* (US)) and one other in the National Herbarium are annotations by Paul Aellen showing that he considered it identical with *Ch. incanum* (Wats.) Heller (better regarded as *Ch. fremontii* Wats. var. *incanum* Wats.), which, in general habit it sometimes resembles. The resemblance, however, goes no further, except as would be expected in species of the same section of the genus.

The leaves of *Ch. nevadense* are much smaller, less numerous, and less conspicuous than is usual in *Ch. fremontii* var. *incanum*, and there are important differences in the inflorescence and seeds. The flowers of var. *incanum* occur in dense terminal panicles of relatively large glomerules, with the branches spicate, not cymose. Those of *Ch. nevadense* occur in small glomerules and as single prominently pedicellate flowers, mixed, in large, very diffuse panicles making up the upper half to three-fourths of the plant. The branching is conspicuously cymose, individual branches becoming even scorpioid. The illustrations will show this. The most obvious recognition mark is the presence of numerous solitary pedicellate flowers.

The type specimen *(Jones 25021)* of *C. capillare* Jones is not very floriferous, but otherwise is identical with *C. nevadense*.

The seeds are very small, 07–0.9 mm. across, and quite thick, with adherent pericarp which can, with difficulty, be rubbed off. Those of *Ch. fremontii* var. *incanum* are larger, 0.9–1 mm. across, with free pericarp.

NEVADA. Washoe Co.: Winnemucca Lake, *Kennedy 1993* (US); Wadsworth, *Jones 25021* (US) (Type of *C. capillare*). Churchill Co.,: 7 mi. e. of Frenchman Station, *Howell 8000* (US). Mineral Co.: 3 mi. s. of Hawthorne, near mouth of Cory Creek, *Archer 6817;* about 50 mi. w. of Tonopah, along highway to Hawthorne, *Henning 231;* mesa near Sodaville, *Tidestrom 10057* (US). Nye Co.: 3-12 mi. s. of Darrough's Hot Springs, *Goodner & Henning 1187;* 20 mi. n. of Tonopah, road to Cloverdale, *Henning 188;* along Cloverdale-Tonopah road, s. of Cloverdale, *Goodner*



Figs. 1-2. *Chenopodium nevadense* Standl., four collections to show variation in habit. 1a. *Lehenbauer 177*, 1b. *Lehenbauer 184*, 2a. *Goodner and Henning 1187*, 2b. *Henning 188*.

& *Henning 741*. Lander Co.: 18 mi. s. of Austin, along Nev. Highway 8-A, *Henning 80;* 35 mi. s. of Austin, along Nev. Highway 8-A, *Henning 98*. Lyon Co.: Petrified forest in Wilson Can., between Smith and Mason Valleys, *Lehenbauer 184, 177*. (All USNA except as indicated). The last collection cited is rather anomalous. It has the erect habit and narrow leaves of *Ch. leptophyllum*, with the open-paniculate inflorescence, single pedicellate flowers from the glomerules, adherent pericarp and thick, small seeds of *Ch. nevadense*.

Ch. nevadense is an inhabitant of dry sandy or rocky, often alkaline soils of central to western and northwestern Nevada.

Atriplex argentea Nutt. ssp. typica Hall & Cl. var. caput-medusae (Eastw.) n. comb.

Atriplex caput-medusae Eastwood, Proc. Calif. Acad. II, 6:316, 1896.

This striking variation certainly deserves varietal rank, even though not sharply set off from the ordinary form of the species. It is distinguished by the form of the mature bracts, which are long stalked and so covered with appendages on the outer faces as to resemble small burs. Hall and Clements (Carn. Inst. Wash. Pub. 326: 285. 1923) reduced this outright to synonymy with ssp. *typica*, a course which I can scarcely follow, since the variety is abundantly distinct, morphologically. If there were not intergrading forms, certainly most workers would regard it as a distinct species.

NEVADA: Mineral Co., mouth of Cory Creek, Wassuk Range, alt. 4,600 ft., *Archer 6828* (USNA); Nye Co., 4-6 mi. n. of Tonopah on road to Cloverdale, *Henning 184* (USNA).

UTAH: San Juan Co., along the San Juan River near Recapture Cr., July 17, 1895, *Eastwood 116* (TYPE) (part in US).

ARIZONA: Apache Co., Painted Desert, *Eastwood* & *Howell 6900* (US).

NEW MEXICO. San Juan Co.: Navajo Indian Res., vic. Shiprock, *Standley 7213* (US); vic. Farmington, *Standley 7086* (US); vic. Cedar Hill, *Standley 8055, 6860* (US). Sandoval Co.: vic. San Ysidro, *Arsene* & *Benedict 17605* (US).

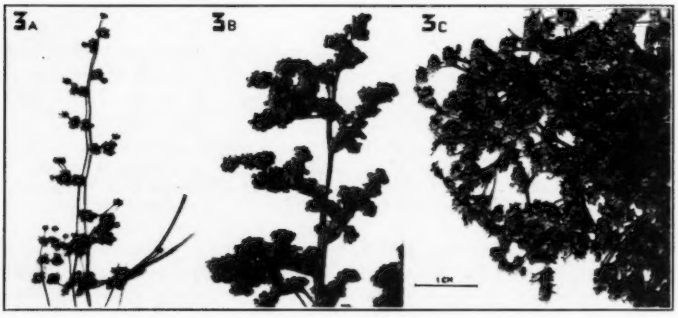


Fig. 3. *Chenopodium nevadense* Standl., detail of inflorescence of three collections, to show variation. 3a. *Lehenbauer 177*, 3b. *Goodner and Henning 1187*, 3c. *Henning 188*.

The following Nevada collections approach var. *caput-medusae*. Lander Co.: mouth of Skull Creek, *Goodner & Goodner 500* (USNA); 35 mi. s. of Austin, *Henning 326* (USNA). Humboldt Co.: Desert Valley, 1-5 mi. e. of Daveytown, 10 mi. e. of Austin Mine, *Train 184* (USNA). Lincoln Co.: Crystal Springs, *Hermansen 77H* (USNA).

ATRIPLEX GARDNERI (Moq.) Standley, N. Am. Fl. **21**:66, 1916.

Obione gardneri Moq. in DC. Prodr. **13**(2):114, 1849.
Atriplex gordoni Hook., Jour. Bot. Kew. Misc. **5**:261, 1853.
Atriplex nuttalli Wats., Proc. Am. Acad. **9**:116, 1874.

There seems, under the Cambridge code, no reason for following Hall and Clements in using the later specific epithet *nuttalli* for this species. There is no doubt whatever as to the application of *gardneri*, and the mere fact that the collector's name was Gordon rather than Gardner does not make the error orthographic. Moquin was obviously under the impression that the plant was collected by someone named Gardner, so the spelling was quite intentional. Until I am satisfied that the subspecies recognized by Hall and Clements represent distinct populations it seems better not to make the combinations for them under *A. gardneri*.

Atriplex patula L. subsp. **hastata** (L.) Hall. & Cl. var. **subspicata** (Nutt.) Proc. Am. Acad. **9**:107, 1874.

Chenopodium subspicatum Nutt., Gen. **1**:199, 1818.
Atriplex carnosa Nels., Bot. Gaz. **34**:361, 1902.
Atriplex subspicata Rydb., Bull. Torr. Cl. **33**:137, 1906.

Though this variety was given no recognition by Hall and Clements, it seems adequately characterized by the densely spicate fleshy bracts. It may be distinguished from ssp. *spicata* by the dentate margins of the fruiting bracts. Represented by *Archer 5875* from Nevada, Douglas Co., 5 mi. w. of Minden, on road to Genoa.

Atriplex phyllostegia (Torr.) Wats. var. **draconis** (Jones) n. comb.

Atriplex draconis M. E. Jones, Contr. W. Bot. **8**:40, 1898.

Characterized by having the fruiting bracts greatly elongated, often united nearly to the summit, with the basal lobes variously suppressed or developed into irregularly toothed or lacerate projections, the faces smooth to prominently appendaged, the pedicels from very short to as long as the bracts, often strongly thickened toward the apex.

NEVADA. Washoe Co.: Wadsworth, near Clarks, alt. 4,300 ft., on sand dunes, June 15, 1897, *M. E. Jones* (US) (part of type). Churchill Co.: near Indian sub-agency, 10 mi. from Fallon, alt. 4,000 ft., *Murphy M85* (USNA). Humboldt Co.: Winnemucca, *Griffiths & Morris 97* (USNA, US); south of Quinn River Crossing, *Griffiths & Morris 108* (USNA, US).

Although *A. draconis* was reduced to *A. phyllostegia* without comment by Jones, himself (Contr. W. Bot. 11: 20, 1903), and Standley N. Am. Fl. 21: 69. 1916), and with some remarks as to the variation of the bracts by Hall and Clements (Carn. Inst. Wash. pub. 326: 267, 1923), the plant is so abundantly distinct that, to me, the question is whether it should not be considered a distinct species. In identifying the Murphy specimen cited above, it

was only after exhausting every other possibility that I associated it with *A. phyllostegia*, even though the latter was abundantly represented in the Indian Drug Plant Project collections, and very easily identified. In appearance they are quite dissimilar.

Analysis of actual characters shows that the differences, though conspicuous, are not especially constant or fundamental, so that I am considering it as of varietal rank. I have not seen staminate plants, but suspect that they would be difficult to tell from *A. phyllostegia*. The fact that the leaves are more persistently mealy, and do not show to any extent the conspicuous parchment-like appearance of *A. phyllostegia* leaves might help. Some plants of the typical form show a tendency toward elongation of the terminal lobes of the bracts, but so far as I have seen, the basal auriculae in mature bracts are always characteristically rounded, and there is little or no tendency to form appendages on the faces. The variation in the bracts of both forms is considerable, but the overlapping is slight. Until further material is available, varietal rank will serve to emphasize the differences without completely dissociating the two.

OXYSTYLIS LUTEA Torr. & Frem.

This species has always been considered strictly endemic to Death Valley and the immediate vicinity including the portion of Nye Co., Nevada, immediately adjacent to California. It was therefore surprising to find it scattered for a distance of several miles on dry open alluvial fans north of the dry lake at McLean, Esmeralda Co., Nevada, alt. 1,630 m., in 1937 (*Fosberg 14275* UP). It was in undisturbed soil with every appearance of being a natural occurrence, though the highway was not far away. A specimen in the National Herbarium (Purpus 6421) is labelled Clayton Valley, Nevada. This lies east of the Silver Peak Range in Esmeralda Co., south of the McLean region.

RHUS TRILOBATA Nutt. ex. T. & G. var. QUINATA Jeps.

Barkley (Ann. Mo. Bot. Gard. 24: 412, 1937) cites two Nevada collections of this variety which his distribution map (p. 401) would indicate must be in Lincoln Co. An abundant stand of a form which seems referable to this variety was observed near Mesquite Springs, 3 mi. w. of Indian Springs, Clark Co. (*Fosberg 14276* UP). The plants are large shrubs, rather rigid, up to 2 m. tall. The shape and cutting of the terminal leaflet indicates that they are nearer to var. *quinata* than to var. *anisophylla*.

Acer nigrum f. var. **pseudoplatanoides** (Pax), n. comb.

Acer saccharinum L. var. *pseudoplatanoides* Pax, Engl. Bot. Jahrb. **7**:242.1886.

A discussion of the reasons for this combination will appear later. The name is needed for immediate use in another paper.

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WASHINGTON, D. C.

Notes and Discussion

Eucalyptus Tree Utilized by Fox Squirrel in California

Jean T. Boulware

The western fox squirrel *(Sciurus niger rufiventer)* was introduced onto the campus of the University of California at Berkeley about 15 years ago. The exact time of introduction and the number introduced are unknown, but the squirrel has multiplied and persisted in this new environment. Here it has been observed to use as a nesting site, and also as a source of food, the blue gum *(Eucalyptus globulus)*, which is itself not native to California, but has been introduced from Australia.

Many varieties of eucalyptus have been introduced into California from Australia in the past century. The distribution of these trees in the United States is limited by temperature; they occur only in a strip varying from 100 to 200 miles in width along the southern and southwestern borders of the United States where the temperature seldom falls below 25°F. or rises above 105°F. Eucalypts grow unusually rapidly and are cultivated as shade, ornamental, and avenue trees, as windbreaks, and as a source of timber, fuel, oil, and honey. The blue gum is probably more extensively planted than all the other eucalypts combined and is one of the fastest growing trees in the world. A grove planted on the Berkeley campus shortly after 1870 contains 110 tall trees, some of which now exceed 200 feet in height.

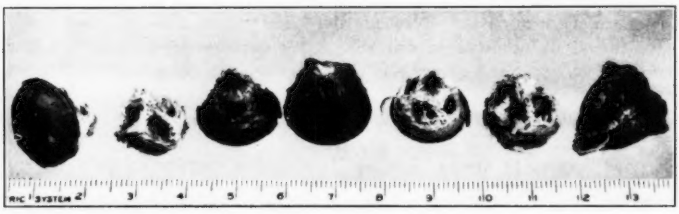

Fig. 1. Fruits of *Eucalyptus globulus* gnawed by *Sciurus niger rufiventer.*

The fox squirrel, in its range throughout the Mississippi Valley, usually dens in decayed cavities of oak, hickory, elm, and other deciduous trees. Also, permanent leaf nests are constructed in the branches of oaks and other trees. Hollows are not available in the potential den trees of the Berkeley campus because bacterial invasion of the heartwood is stopped by tree surgery and by removal of dead limbs. The mild winters perhaps obviate the need for dens. Be this as it may, the one nest found was a permanent leaf nest, in the eucalyptus.

In the grove of blue gums on the campus, one tall tree with a diameter of 7 feet at chest height stands a short distance away from the others. On March 7, 1941, a fox squirrel nest was found in this tree 15 feet above the ground in a crotch formed by a narrow forking of the thick trunk. The nest was composed entirely of eucalyptus bark. The bark of the blue gum is deciduous and flakes off in patches and long thin strips. The roughly spherical nest was somewhat concealed by strips of bark which had lodged in the crotch. The outside of the nest had a diameter of about 40 cm., and the ellipsoidal cavity a volume of approximately 2,100 cc. A hole, which overhanging strips of bark reduced to a width of 8 cm., led into the nest. The cavity was lined with finely shredded

bark; larger pieces and strips of bark, thickly matted around the lining, afforded the nest ample protection from wind and rain. The persistent dry bark on the trunk beneath the entrance was much scratched, indicating the route of the squirrels up and down the tree. On top of the nest were several sprigs with gnawed stems bearing the capsular fruits of the eucalyptus.

When the nest was first examined, on March 7, an adult squirrel ran out of the entrance and up the tree. I then inserted my hand into the hole and my third finger was grazed by incisor teeth. Also, I heard low growling noises within the nest cavity. Further investigation was terminated by the unsympathetic attitude of a campus policeman. At the time of the second examination, on March 18, three young about 4 weeks old, but no adults, were found in the nest.

On the Berkeley campus, the fruit of the blue gum is an item of food of the fox squirrel. Numerous capsules gnawed by squirrels (Fig. 1) were found beneath the gum trees. The fruit is warty and covered with bluish white wax that bears the strong scent and taste of eucalyptol, chief ingredient of the oil of the blue gum. The pungent odor of this oil seems not to discourage the squirrel in its search for the small, black, pyramidal seeds contained within the four or five cells of the capsule. The squirrel scampers out to the end of a eucalyptus branch and swings precariously as it chews off a capsule from a fruited cluster. With a capsule in its mouth, it frequently returns to some favorite spot farther in on the limb and, rotating the capsule rapidly in its paws, chews into the outer green and woody parts from the stem end. Discarding the reddish chaff, the squirrel eats the seeds. This process was observed several times in April and May. A similar procedure has been noted by Luther Little (Journ. Mammalogy **15**:158-159) as employed by the Anthony gray squirrel *(Sciurus griseus anthonyi)* in South Pasadena, California.

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Berkeley, California.

Book Reviews

MARINE LIFE IN TEXAS WATERS. By Clyde T. Reed. xii+88. 25 plates. Texas Academy Publications in Natural History. Houston, 1941. Anson Jones Press. $1.00.

This is the second of a non-technical "series of brochures purposed to present the scientific scene with accuracy and interest . . ." fostered by the Texas Academy of Science. In the foreword the Editorial Board states that the title is more inclusive than the material included. A descriptive title would be, "Miscellaneous observations on elementary marine biology with taxonomic lists of some groups of animals and plants seen on the Texas Coast by the author in the past fifteen years." The volume is surprisingly short, the actual text, exclusive of plates and appendices, being only fifty-seven pages of print. Naturally, many things that we would like to see are left out. The chief lack is a general description of the Texas Coast, its large bay area, barrier islands and sandy shores. I would have liked to have seen at least a short discussion of the extreme variation in salinity of Texas bay waters and some remarks on the periodically oversaline Laguna Madre, which differs from any other habitat of the United States Coast.

The work has five main headings, an introduction called, "Going Down to the Sea" and a discussion of the common marine life of Texas divided into four parts, namely, Plankton, Staton, Vagon and Necton. The writer is at his best when describing the marine life he has observed. The volume is illustrated with twenty-five plates of rather good quality.

There are ten appendices. One, a chart of heights and depths of trees, buildings, the seas, mountains, cloud layers and the stratosphere, will be of special interest to beginners. Some of the others, such as Chief Commercial Fishes, Game Fish, List of Mollusca, Sharks and Rays, and Classification of Algae will always serve as guides to students and specialists beginning studies of the varied life of this coast. Needless to say these non-committal lists of flora and fauna are not nearly so valuable as annotated check lists would have been. It seems to me that the list of enemies of the oyster is a matter too small and too specialized for inclusion as an appendix in a work of this type.

Professor Reed has actively concerned himself with all of the groups of animals and plants discussed, a fact which is indicative of the great energy poured forth in acquiring the necessary knowledge for preparation of the volume. This is a refreshing thing to contemplate in our age of specialists, but, doubtless as a result of it, certain errors have slipped in. There is very inconsistent use of author's full names and abbreviations of variable length following species names. There are some unfortunate misspellings or typographical errors, especially in the names of fishes. In one place an author's name is italicised, in another a comma is placed between the specific and subspecific name, and one gastropod is given a Latin name consisting of four words. Probably several minor errors would have been avoided if the author had seen the proofs, but, unfortunately, he did not see them.

It is stated in the text that *Octopus vulgaris* up to a width of three feet stretched have been reported from this coast. On page five an illustration of a specimen from the reviewer's collection is given. The animal measures five feet and two inches in width with arms outstretched. The common coon oyster is listed as *Ostrea frons*. All the coon oysters I have seen in Texas are variants of *Ostrea virginica* and the correctness of the other designation is extremely doubtful. In the table of oyster enemies the salinity figures are given as parts per million, whereas parts per thousand were intended.

The picture of the river shrimp, *Macrobrachium jamaicense*, on page thirty-six is labeled *M. ohionis*. *Penaeus brasiliensis* is listed as one of the commercial shrimp of Texas. It was shown a few years ago that this species does not occur here. The Texas species is *P. aztecus*, and there are unpublished data that another closely related shrimp occurs.

Evidently the author followed the check list of Jordan, Evermann and Clark in naming the fishes, resulting in some names not used by American ichthyologists. I suspect that the list of sharks and rays is made up of species seen by the author, rather than taken by him, as is stated, for it is hard to believe that one collector could have taken such rare and hard-to-catch elasmobranchs as the Thresher Shark, Mackerel Shark, Angel Shark and the Great Manta. On page twenty there is a plate of a scorpionfish labeled *Scorpaena plumieri*. The picture is that of a specimen I am using as the paratype of a new species, a fact pointed out to the author before his work was published. *Istiophorus volador* is listed as the common Texas sailfish. Leaving out the question of validity of that species, the common Texas sailfish is *I. americanus*. The reviewer has grave doubts that the inclusion of the swordfish, *Xiphias gladius*, on the list of Texas game fishes is based on an authentic record. *Cynoscion nothus* is included in the list of commercial fishes, whereas *C. arenarius* should have been listed instead. On page sixty-four the statement is made that the death of large numbers of fish on the Texas Coast in 1935 was caused by a flowering of the diatom, *Asterionella japonica*, which pierced the gills and obstructed respiration. To the reviewer, that theory is unacceptable.

The common porpoise is correctly listed as *Tursiops truncatus* in the text, while in the appendix it is incorrectly called *Phocaena phocaena*.

The preparation of this work is no small achievement for one man, in spite of some of the errors and shortcomings pointed out here. It is the first broad attempt at a description of Texas marine life and it will stand from now on as a starting place and point of discussion for work on any life group in the Western Gulf of Mexico.

—GORDON GUNTER.

ELEMENTS OF GENETICS. By Edward C. Colin. The Blakiston Company, Philadelphia, 1941. xii+386 pp. $3.00.

The stated purpose of this text is the presentation of the elementary principles of the science of genetics "with special emphasis upon applications to man." The author accomplishes his purpose, and in doing so he employs a manner of exposition which is commendable. The subjects are treated in such style that even the beginning student in biology might read the book with interest, understanding, and profit.

The author devotes much space to discussions of characters in man which have a genetic basis. In addition to two full chapters which deal exclusively with human genetics, he introduces human characters as examples of the points developed in other chapters. The historical facts concerning Mendel and his work are treated in a somewhat fuller fashion than they have been in other comparable texts. These things have not been done without sacrifice, however. Some of the topics are over-simplified, and other important ones are given scant notice. The paucity of material concerning the economic importance of genetics is especially noticeable. Most of the fundamentals are covered, however, and they are done sufficiently well to allow the profitable use of the text in courses in genetics which are supposed to be "cultural."

The figures used are clear, and the index, apparently, is full. There is appended a glossary of terms which should be valuable.—E. LAWRENCE POWERS, JR.

SCIENCE IN PROGRESS. Second Series. Edited by George A. Baitsell. Yale University Press, New Haven, Connecticut, 1940. xii + 317 pp., 129 figs. $4.00.

Equal to the first series in every respect, the present volume is made up of the National Lectureships sponsored in 1939 and 1940 by the Society of the Sigma Xi. However, a somewhat different selection is offered. In chapter I "The Experimental Alteration of Heredity," L. J. Stadler reviews the two principal types of hereditary changes and the agents employed in their experimental production. F. W. Went attempts "to present a synthetic picture of a plant in its growth and development" in his discussion of "The Regulation of Plant Growth" and predicts the eventual

emergence of the new science of plant engineering. The effectiveness of the comparative approach to scientific problems, other than morphological ones, is demonstrated by J. F. Fulton in his review of "Experimental Studies on the Functions of the Frontal Lobes in Monkeys, Chimpanzees, and Man." Finally, D. A. MacInnes assures the reader in his chapter on "The Motions of Ions and Proteins in Electric Fields" that increased knowledge concerning the physical chemistry of proteins will throw considerable light on their functions. The remaining chapters represent certain aspects of the physical and engineering sciences.

As the rather artificial boundaries of scientific disciplines are being broken down, the new outlook envisaged by the contributors may well be regarded as the expression of a unifying endeavor to check the appalling advances in the direction of overspecialization. This effort in itself is a noteworthy enterprise. To it may also be added the great service to humanity rendered by the Society of the Sigma Xi, founded for the Promotion of Research in Science, through its other recently acquired function of the "Dispersal of Knowledge."—THEO. JUST.

AN INTRODUCTION TO ENTOMOLOGY. By John Henry Comstock. Comstock Publishing Co., Ithaca, N. Y., 1940. Ninth edition revised. xix + 1064 pp., frontispiece, 1228 figs. $5.00.

The fact that a ninth edition is now available bespeaks at once the quality of the book and its continued favorable reception by entomologists. Compared with previous editions, the present one offers a revised treatment of the parasitic Hymenoptera together with improved keys, all contributed by Dr. Henry K. Townes. The superior grade of paper used in the printing of this edition is another welcome improvement. In its new form this classic textbook preserves its original character and retains justly its place in the field.—THEO. JUST.

A MANUAL OF AQUATIC PLANTS. By Norman C. Fassett. McGraw-Hill Book Co., New York, 1940. viii + 382 pp., 226 illustrations. $4.00.

The content of most manuals is clearly defined taxonomically and geographically. By comparison "A Manual of Aquatic Plants" is ecologically confined to plants growing in certain aquatic habitats (saline, tidal, and bog habitats are excluded), and geographically to the northeastern United States. The plants treated were no doubt selected on the basis of the author's definition of an aquatic "as a plant that may, under normal conditions, germinate and grow with at least its base in the water and is large enough to be seen with the naked eye." Some algae, mosses, liverworts (treated by Dr. Pauline Snure), ferns and fern allies are therefore included, but the bulk of the book is devoted to flowering plants. Excellent, and for most part original, drawings of the habits of many species or, at least, of their important diagnostic characters accompany the descriptions and keys. The practical value of the book is enhanced by the data summarized in the appendix and pertaining to the "Use of Aquatic Plants by Birds and Mammals," "The Relation of Plants to Fish," and a glossary. Throughout the book much care has been given to the preparation of extensive keys, often based on the characters of sterile plants, to facilitate their identification. This extremely useful book is likely to stimulate further interest in aquatic plants.—THEO. JUST.

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Contents

The Role of Territory in Bird Life—*Margaret Morse Nice* 441

British Columbia Dragonflies (Odonata), with Notes on Distribution and Habits (With Descriptions of Two New Nymphs by *E. M. Walker*)—*F. C. Whitehouse* 488

Taxonomic and Bionomic Notes on the Grasshopper Melanoplus impudicus Scudder (Orthoptera: Acrididae)—*Ashley B. Gurney* 558

Geographic Variation in Garter Snakes of the Species Thamnophis sirtalis in the Pacific Coast Region of North America—*Henry S. Fitch* 570

Winter Habits of the Red-Eyed Towhee in Eastern Kentucky—*Roger W. Barbour* 593

Microdalyellia gilesi—n. sp., a New Turbellarian Worm from Mountain Lake, Virginia—*E. Ruffin Jones, Jr.* and *Wayland J. Hayes, Jr.* 596

Twenty Years' Statistical Studies of Marine Plankton Dinoflagellates of Southern California—*Winfred Emory Allen* 603

Seasonal Food-Cycle Dynamics in a Senescent Lake—*Raymond L. Lindeman* 636

Studies in Ohio Floristics. I. Vegetation of Ohio Bogs—*Clyde H. Jones* 674

Notes on North American Plants—I.—*F. R. Fosberg* 690

Notes and Discussion:
Eucalyptus Tree Utilized by Fox Squirrel in California—*Jean T. Boulware* 696

Book Reviews 698

Vol. 26 NOVEMBER, 1941 No. 3

REPRINT-SERIES

(Reprints 1, 2, 3 were issued with volume 2, reprint 4 with volume 3 and reprint 5 with volume 5).

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